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NINTH ANNUAL 1970

Cornell Laboratory of Ornithology

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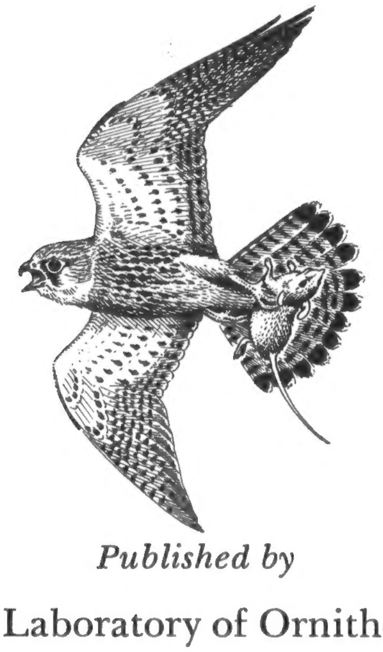
1970

Edited by
OLIN SEWALL PETTINGILL, JR.
and
DOUGLAS A. LANCASTER



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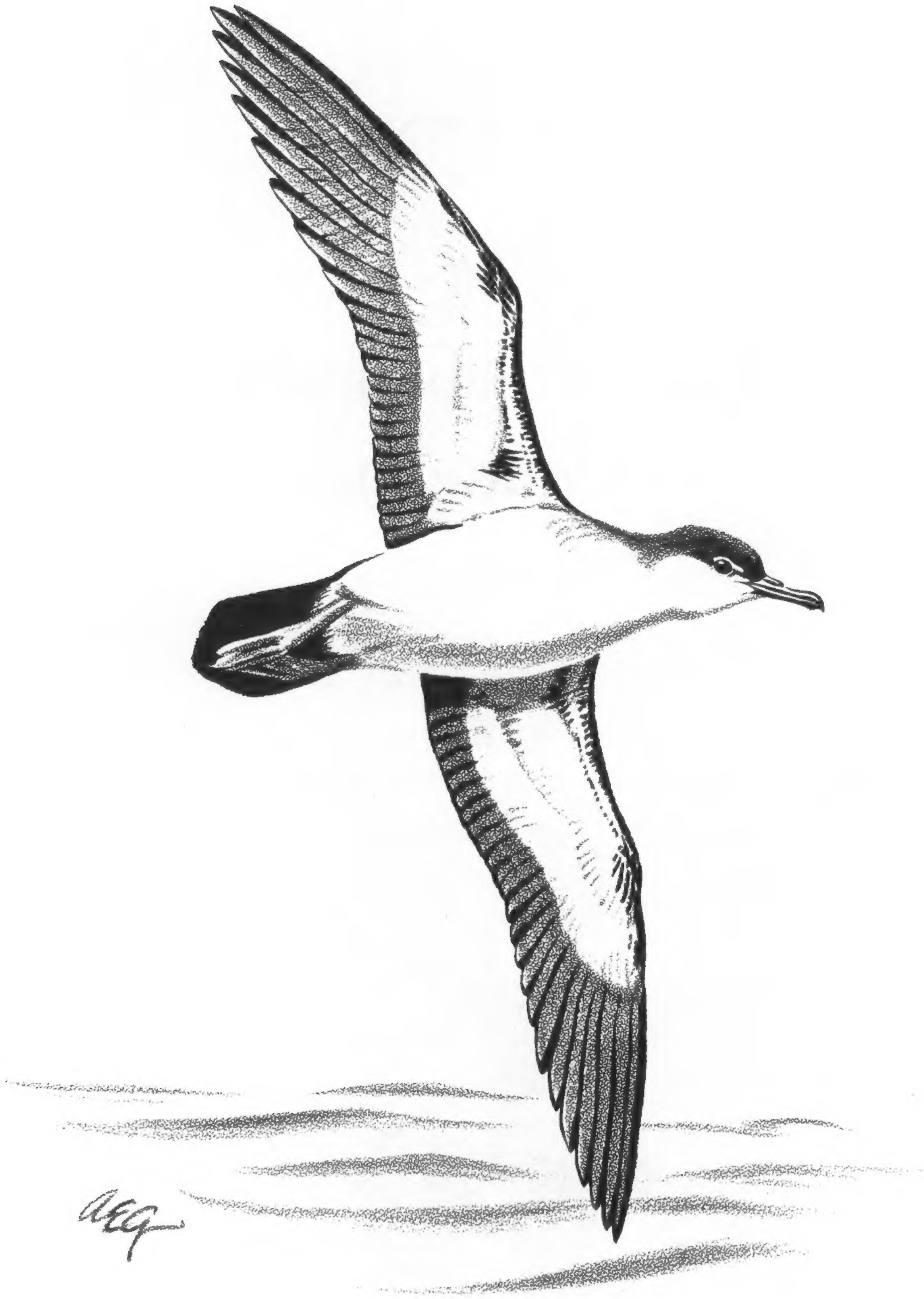

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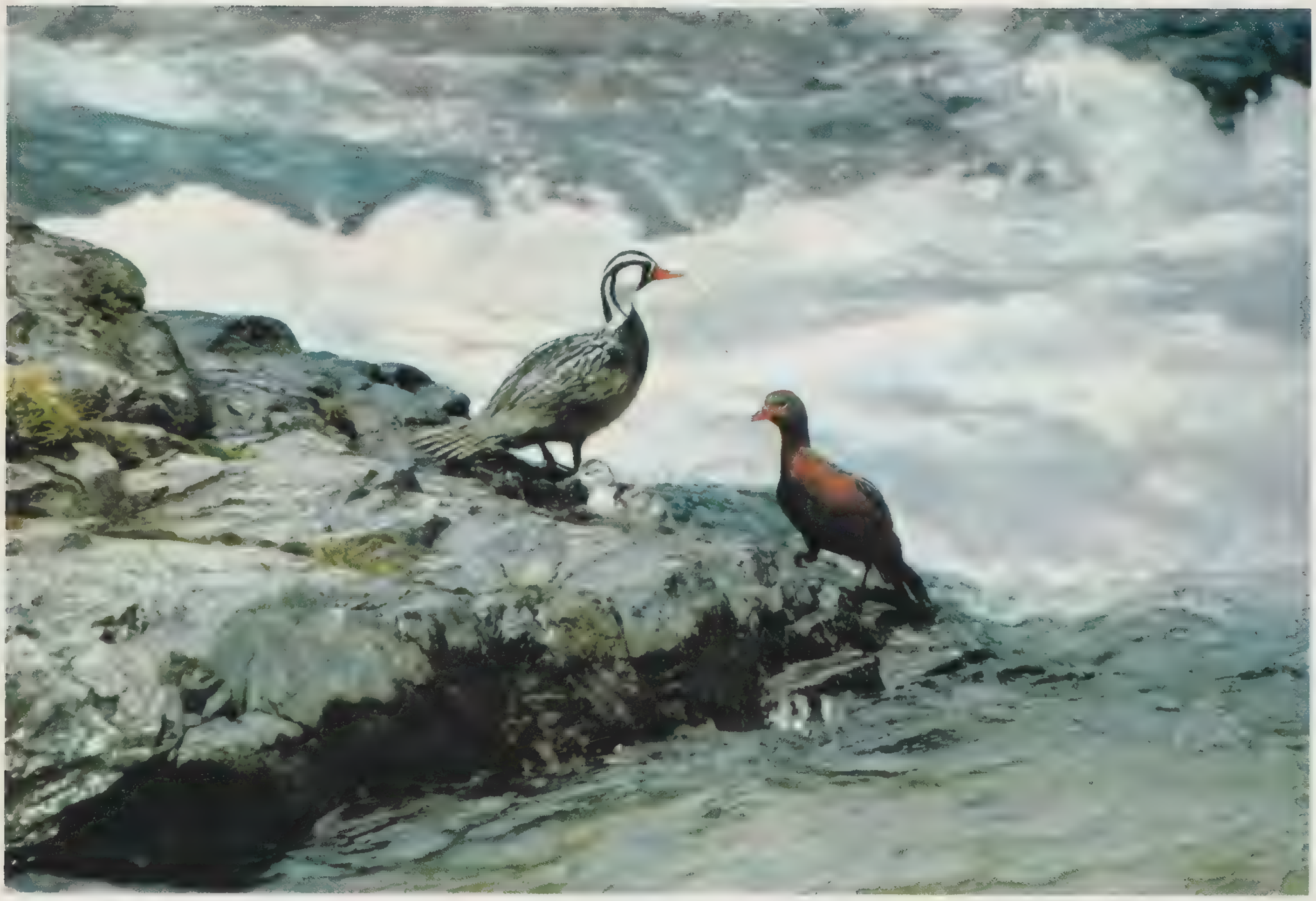
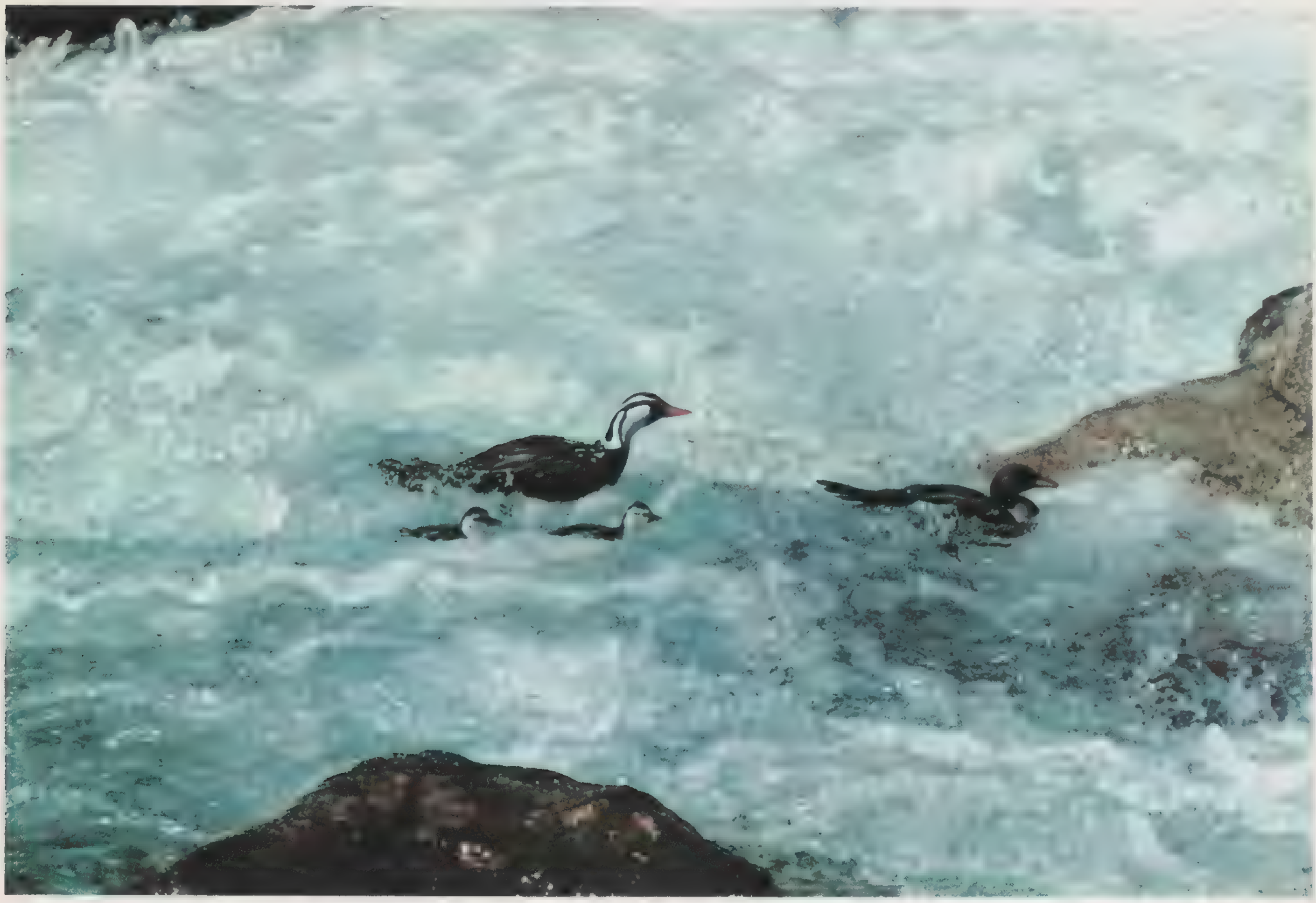


Plate I. A family of Torrent Ducks, *Merganetta armata,* pauses in the sun *(above)* and navigates the rapids of the Rio El Ternero *(below).*



A STUDY OF NESTING TORRENT DUCKS IN THE ANDES

by

GEORGE M. MOFFETT, JR.

Photographs by the author

September heralds the advent of spring in the Rio Negro Province of western Argentina. Here, in September, the peaks of the Andes, rising to only about 6,000 feet, are still white with snow as are the pine and beech covered slopes and valleys and the scrubby, treeless windswept plains that lie between the rugged cordilleras. Immediately to the west, the Cerro Nevada forms the boundary between Chile and Argentina; to the south, lies Patagonia; to the north, about 80 miles distant, is Lake Nahuel Huapi with its alpine resort of Bariloche; and to the east, just over the bare mountains, stretch the pampas. El Bolson is the principal town in the extreme western part of Rio Negro Province.

In September 1968, Marvin Cecil and I came to an area near El Bolson to search for Torrent Ducks (*Merganetta armata*): he, to take eggs back to Florida to hatch them at the Caribbean Gardens in Naples; I, to photograph the birds. We searched mainly along the Rio El Ternero, a very fast moving stream, about 18 miles in length, on the western divide of the Andes. I tramped along it and camped beside it from September to mid-November, observing and photographing Torrent Ducks (Figures 1 and 2).

The Torrent Duck lives along the rapid mountain streams of the Andes from Venezuela to Tierra del Fuego. Only slightly larger than the Blue-winged Teal (*Anas discors*), the Torrent Duck possesses a number of unusual features that set it apart from all the others. The slender narrow body undoubtedly allows the bird to move underwater against strong currents with ease. A long tail with stiff rectrices aids its propulsion through the water. A narrow, flexible, almost rubber-like bill enables it to feed among the crevices of submerged rocks. There is a pronounced sexual dimorphism—a difference in the appearance of the sexes. The larger male has a boldly marked plumage. The head and neck are white with several black stripes (see Plate I); the upper back is white fading into black and white streaking; and the underparts are dark brown streaked with black. The blue wings possess a bright green speculum margined above and below with white. The bill is bright red; the legs a duller red. In contrast, the female is uniformly gray above and rich brown below.

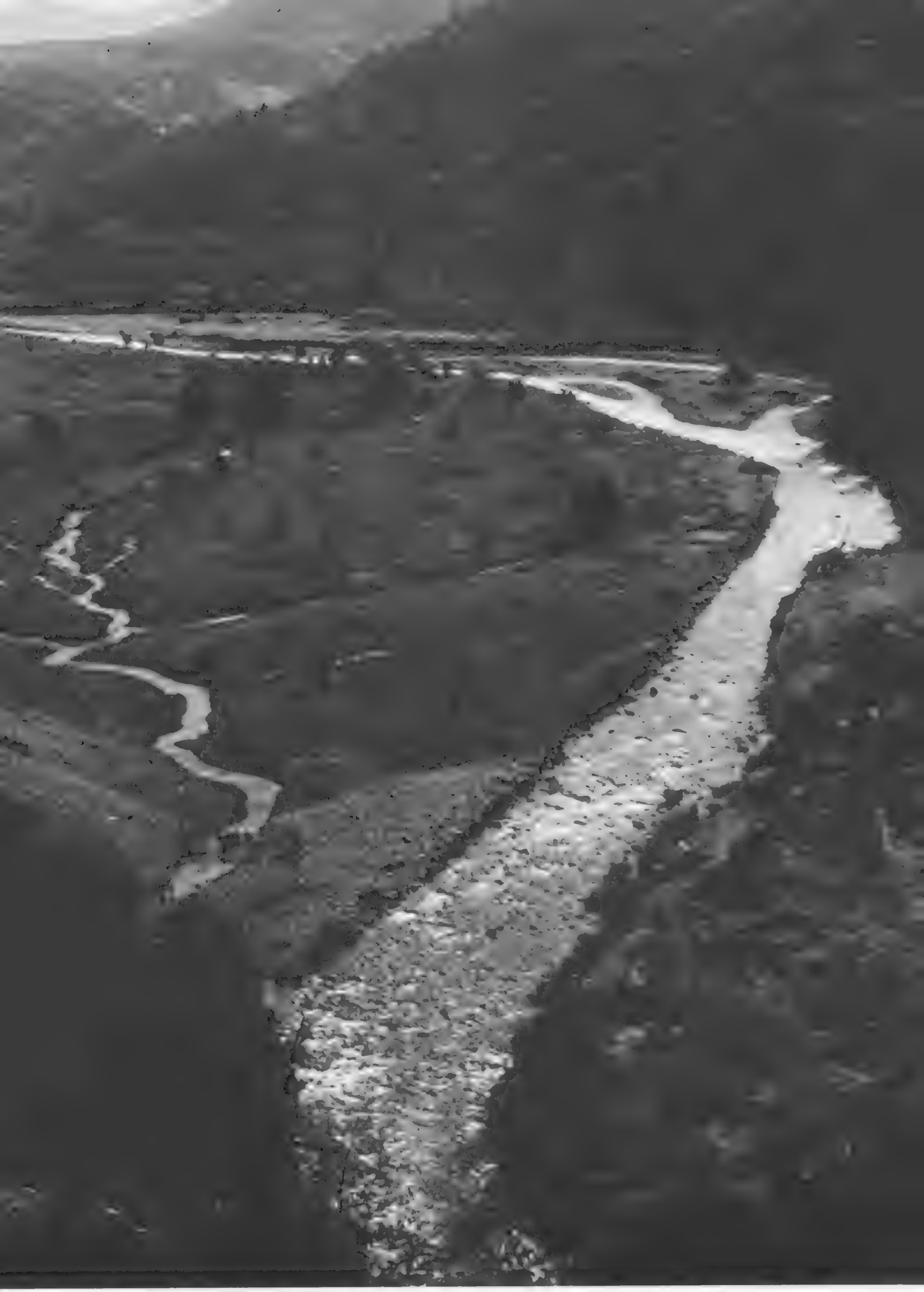


Figure 1. The Rio El Ternero, with its rushing waters, comprises a typical habitat for the Torrent Duck. Here, in Rio Negro Province, Argentina, pines and beech cover the mountain slopes and valleys, intermingled with treeless, scrubby plains between the rugged cordilleras.

Opinions differ about the taxonomic position of the Torrent Ducks. This species, with its six geographical races, warrants a separate taxonomic grouping according to Woolfenden (1961) who maintains that taxonomists should place it in a separate tribe. Others (Delacour, 1954; Niethammer, 1952) regard the Torrent Duck as an aberrant bird with clear affinities to the tribe of ducks that includes teal, pintails, mallards, and many others. Johnsgard (1966), on the other hand, believes that it might well be a member of the perching duck tribe (Cairinini).

Regardless of its relationships with other ducks, the Torrent Duck features a highly specialized way of living in its extremely restricted environment.

Few nests of these shy birds have been recorded. Johnson (1965) lists only four verified nests, two in Chile and two in Colombia. The most recent, in 1960, he discovered himself. Furthermore, no one has ever kept a Torrent Duck alive for any length of time outside its habitat. Peter Scott had one at the Wildfowl Trust the longest, I believe. He wrote me in April 1969: "We had a male Peruvian Torrent Duck here for about five months. He remained terribly wild and never really recovered the waterproofing of his feathers. Alas, he died last week." Marvin Cecil hoped to rear the young in Florida.

Our first job was to find a nest. For a month prior to our arrival in the El Ternero River area, a taxidermist, Andor Kovacs, and four of his sons, all guides and collectors, had been engaged to scout the rivers around El Bolson, where Torrent Ducks frequently occur.

On the first day after our arrival at El Bolson, the Kovacses took us to a lumber camp on the El Ternero, belonging to Senor Drago Milinkovic. He led us to a place a quarter of a mile upstream where the river, only 20 or 30 feet across, entered a gorge and raced in a fury of white water amid boulders and rocks, showing that its name, meaning the Young Bull, is most appropriate. From a steep bank a large, thick-trunked coihué tree (*Nothofagus dombeyi*) leaned out over the river. Andor Kovacs pointed to two cavities on the underside of the trunk, right over and about 15 feet above the surface of the water. He told us that there might be a nest in one of the cavities (Figure 3). After a struggle, Marvin Cecil roped himself up to one of the holes and found inside four eggs covered with down. We were elated, and yet we could not be sure it was the nest of a Torrent Duck. There was the possibility that the nest was occupied by a pair of Ringed Kingfishers (*Ceryle torquata*) because these two supposedly exchange nest burrows at times (Johnson, 1965). We had seen the beautiful kingfisher on our climb up the stream; we had not yet seen a Torrent Duck.

We returned to the lumber camp and set off again almost immediately in a drizzle to scout another possible nest three miles downstream. The drizzle soon turned to rain. We had only one fleeting glimpse of a Torrent Duck which, alerted by our presence, left his perch on a rock and floated off down the fast flowing river. The alleged nest site, a cavity in a coihué tree, was empty. An *asado,* beef grilled over log embers, in a coihué grove was the only respite in the long arduous trip back.

While the others hunted for nests, I spent the next few days, camera in hand, fruitlessly chasing after Torrent Ducks along the El Ternero. In covering some three miles of river during the course of a day, I usually sighted these

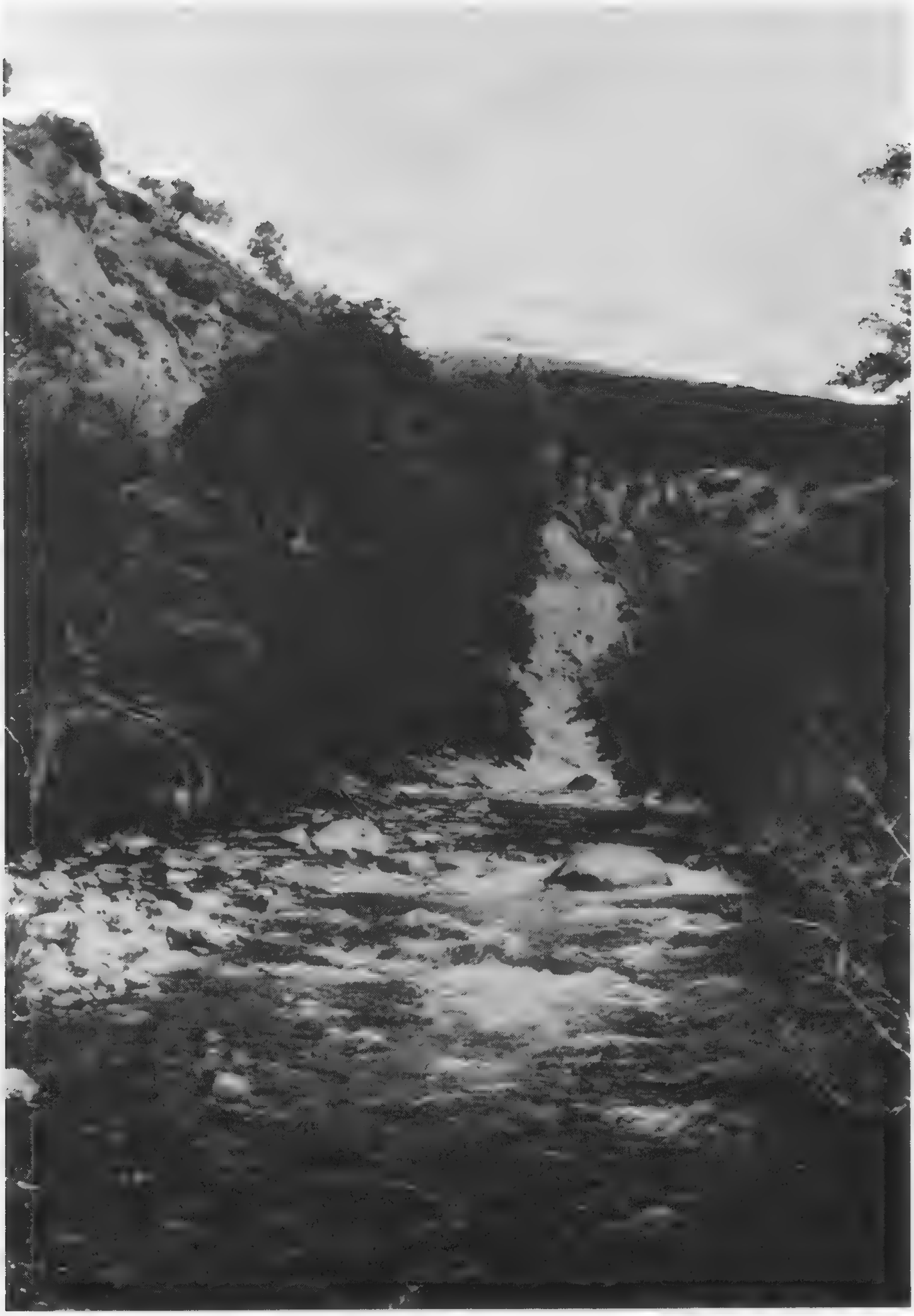


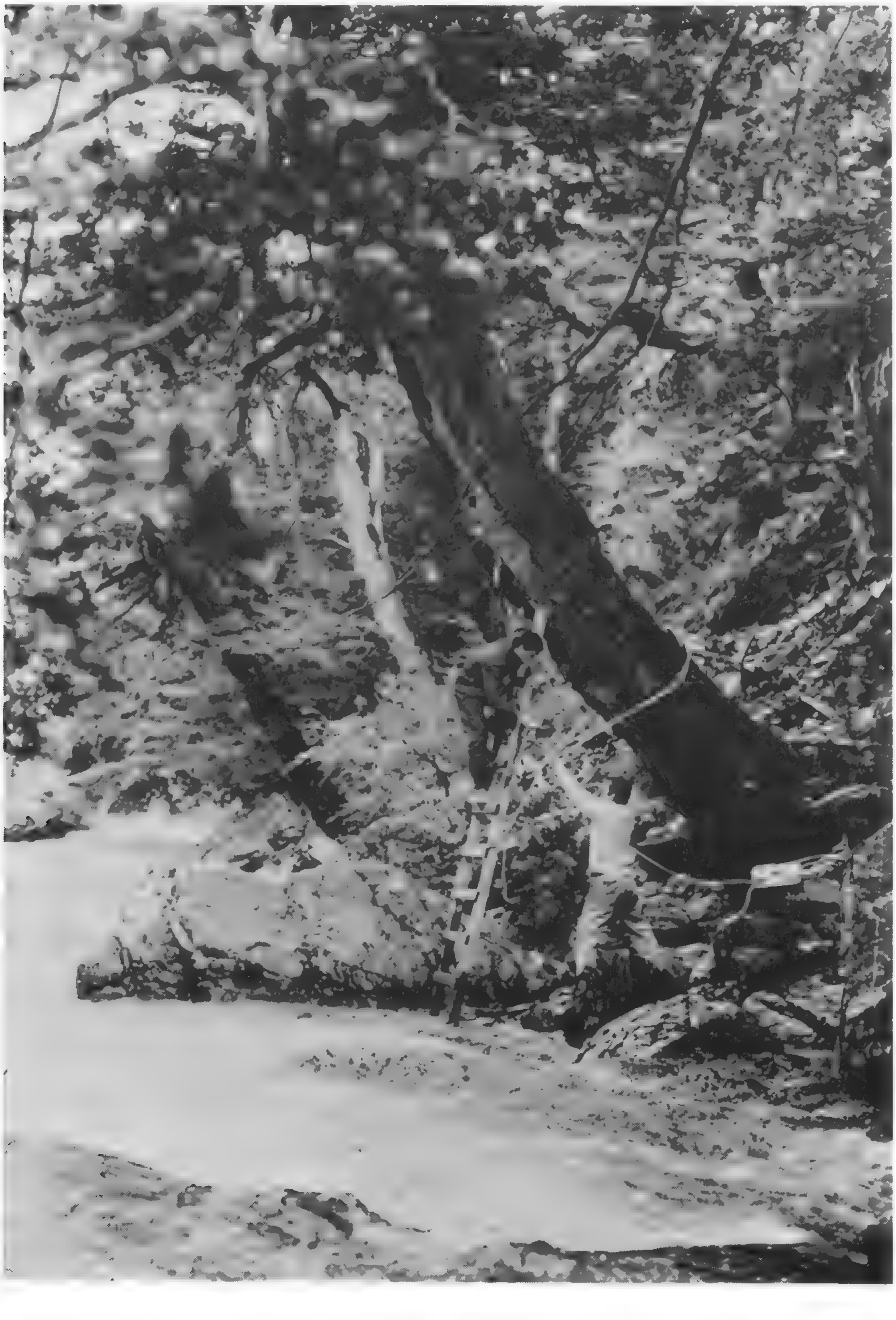
Figure 2. The Rio El Ternero, site of the study of the Torrent Duck. The waters here run off the slopes of the Andes, still covered with snow in September at 6,000 feet.

wary birds about a dozen times and then only through binoculars at a distance. My best view occurred when I spotted a male moving upstream toward me, feeding mostly along the sides of the river where the water ran less swiftly. In half an hour of diving and surfacing he advanced about 100 yards. He spent an average of about seven seconds underwater and about half as much time on the surface.

Meanwhile the news that the Kovacses had located another nest far downstream led me to concentrate on hunting and forget the camera for the time being. Having noticed several boulders in a certain part of the river regularly favored by one pair of Torrent Ducks, I decided to map that portion of the river and record each sighting of them. Using the sun as a compass and a camera range finder as a measuring rod, I made a reasonably accurate map of what appeared to be the pair's territory. I numbered all the boulders, shoals, overhanging trees, and other landmarks, and whenever I saw one of the pair in a particular spot, I noted the location and time and the direction in which it left or arrived at the spot.

My notes soon showed that their territory included about six-tenths of a mile of river where it flowed at an average rate of six feet per second. The

Figure 3. Locating a Torrent Duck nest in the cavity of a coihué tree beside the El Ternero. This one contained four down-covered eggs.



elevation was about 1,980 feet, and the water temperature about 5°C. Working along this section I gradually narrowed the territory to 1,750 feet of river where I most frequently saw the pair. Then I built a blind, pitched a tent as refuge from rain and snow, and waited.

The pair spent much of the time along a stretch of river where the boulders were numerous and where trees from the heavily wooded banks overhung the water. One day I followed the female to this area, and as I watched from the opposite bank, she suddenly leaped up onto the dead limb of a coihué tree that slanted down toward the water, and moved up and down the limb sidewise in a nervous manner. She faced upstream and made frequent head-and-neck bobbing movements which both birds often did before taking off. But she did not take off. She made head-pumping movements as if to leap, then moved up the limb, made more head-pumping movements, moved down the limb, and then repeated the behavior. Finally, she jumped into the water, swam a few yards upstream, and then, all at once, leaped to the bank on the far side of a coihué—out of sight.

I dropped my camera, grabbed my binoculars, and made my way along the bank upstream until I was opposite the place where the female had disappeared. Soon I spotted her through the brush and leaves of the overhanging trees. She was right next to the coihué in a cavity between roots uncovered by the erosion of the river bank. I watched for half an hour. She never moved and neither did I. This nest was so much more exposed than I had expected.

After a while I spotted the male on a boulder downstream, asleep with his bill tucked under his right wing. I moved down the bank to a point halfway between the nest and the male and tried to watch them both. I was looking at the female when something whizzed by me, not five yards from my nose. It was the male in full flight, calling *wheek wheek* in a high-pitched, single-syllabic call. He flew fast and low and in seconds was around the bend of the river and out of sight.

The Torrent Ducks always flew low and followed the river. This I found to be true of all the Torrent Ducks I watched. They flew along the axis of the river no matter how circuitous its course.

Although I did not see the female leave the nest, she must have followed him. When I looked again, she was gone. I put on my waders and with difficulty forded the stream. Water dripped from the high embankment. Tiny, vermilion-colored flowers grew in the mossy crevices of the ledges. I found a foothold and, using the exposed roots as handholds, hoisted myself up to the level of the cavity, about nine feet above the river. Two eggs lay in a shallow scrape. They were buff in color and about the size of a large chicken egg. There was no down at all in the scrape.

This nest was new; the clutch was not complete. I could not believe my luck. Here was a chance to discover the incubation period. Although I had been told it was from 21 to 24 days, the incubation period was actually unknown. And I would have an opportunity to observe the behavior of the downy chicks when they first entered the raging river—this too was unknown. Although the Kovacses had already found two nests, each contained four eggs embedded in down. Both were too far along to help in determining the incubation period.

Habitat, Locomotion, and Feeding

On the following days I observed Torrent Ducks for many hours. Their most notable characteristic is their ability to swim against strong currents, either underwater or on the surface. The rivers and streams they usually inhabit flow at the rate of from six to eight feet per second, but they can make headway against water flowing at 10 feet per second (Johnsgard, 1966).

Torrent Ducks live in swift mountain streams that must contain submerged and partly submerged boulders, for only in such a stream is the water sufficiently oxygenated to support the stonefly larvae (*Rheophila*) on which the Torrent Ducks feed almost exclusively. They dive underwater and extract the larvae from the cracks and crannies among the rocks and stones on the bottom with their bills—narrow, flexible, and edged with serrations.

They expend considerable energy in feeding. I once observed a female Torrent Duck feed vigorously upstream for an hour and a half, where the surface velocity was over seven feet per second. In a stream of even greater velocity, ten feet per second, ". . . a bird simply maintaining its submerged position in the water for sixteen seconds would have to perform the equivalent effort of swimming 160 feet underwater!" (Johnsgard, 1966). While the El Ternero never flowed quite that swiftly, I saw both the male and female feeding underwater for 16 seconds, and sometimes much longer.

As is typical of any species whose habits are unusual yet little known, explanations, suggestions, and even myths abound around the Torrent Duck. Some authors have suggested that the carpal spurs, present in both male and female Torrent Ducks, function in anchoring the birds to the bottom during feeding. While it is difficult to watch them underwater, I did have some views and I never saw any evidence of this. Johnsgard (1966) cautiously stated that, ". . . the adults appeared to hold their wings open slightly when swimming underwater, probably for steering purposes rather than propulsion." In the birds I observed swimming underwater the wings were always folded close to their bodies and played no part in underwater movement. Their bodies are narrow and elongated. They propel themselves through the water with a large powerful tail and with huge feet. One explanation for the size of the Torrent Duck egg, large in proportion to the body, is that it must accommodate the large webbed feet of the downy young which, as we shall see, needs them very early in life.

So much has been written about the Torrent Duck's ability to swim against strong currents that one might think the bird spends most of its waking hours performing this strenuous activity. Such is not the case. The Torrent Duck prefers to expend the least amount of energy possible when traveling along the river. Except for certain circumstances, I never saw the male or female swim upstream underwater very far—usually less than 10 feet. When underwater, it is mostly a question of the duck holding its own against the current. In their usual method of going upriver, they skitter across the surface, using their tails as a kind of skulling oar and the feet as paddles. If they want to cover long distances, they, of course, fly. While swimming upstream they usually keep to the sides of the river where the current is less swift. But their chief method of saving energy lies in their ability to take advantage of the reverse eddies and still water behind rocks and boulders. The pair I watched closely commonly bobbed placidly about in the gentle swirl behind a boulder where the water piled three feet high in front of it from the force of the river. The male and female also spent considerable time standing on rocks partially or totally submerged. As I watched them standing on submerged rocks, it seemed remarkable that they could maintain their balance with apparent ease as the water piled up on their breasts. They used their strong tails for balance—as a counter weight, not for support as one leg of a tripod—and held on to the slippery rocks with their feet and sharp toenails.

After suitable rest periods, they went back to the river to continue their feeding, and it was amusing to see how differently the male and female entered the water from a rock perch. The male always stuck his neck out and teetered over the brink, as if coiling his springs for a mighty leap out into the torrent. His was the racing start, with the accompanying splash (Figure 4). The female, on the other hand, rarely jumped into the water. She slowly eased herself in without commotion or fuss.

When feeding, the pair almost always worked their way upstream from the nest area, sometimes almost as much as half a mile. After they had fed enough,

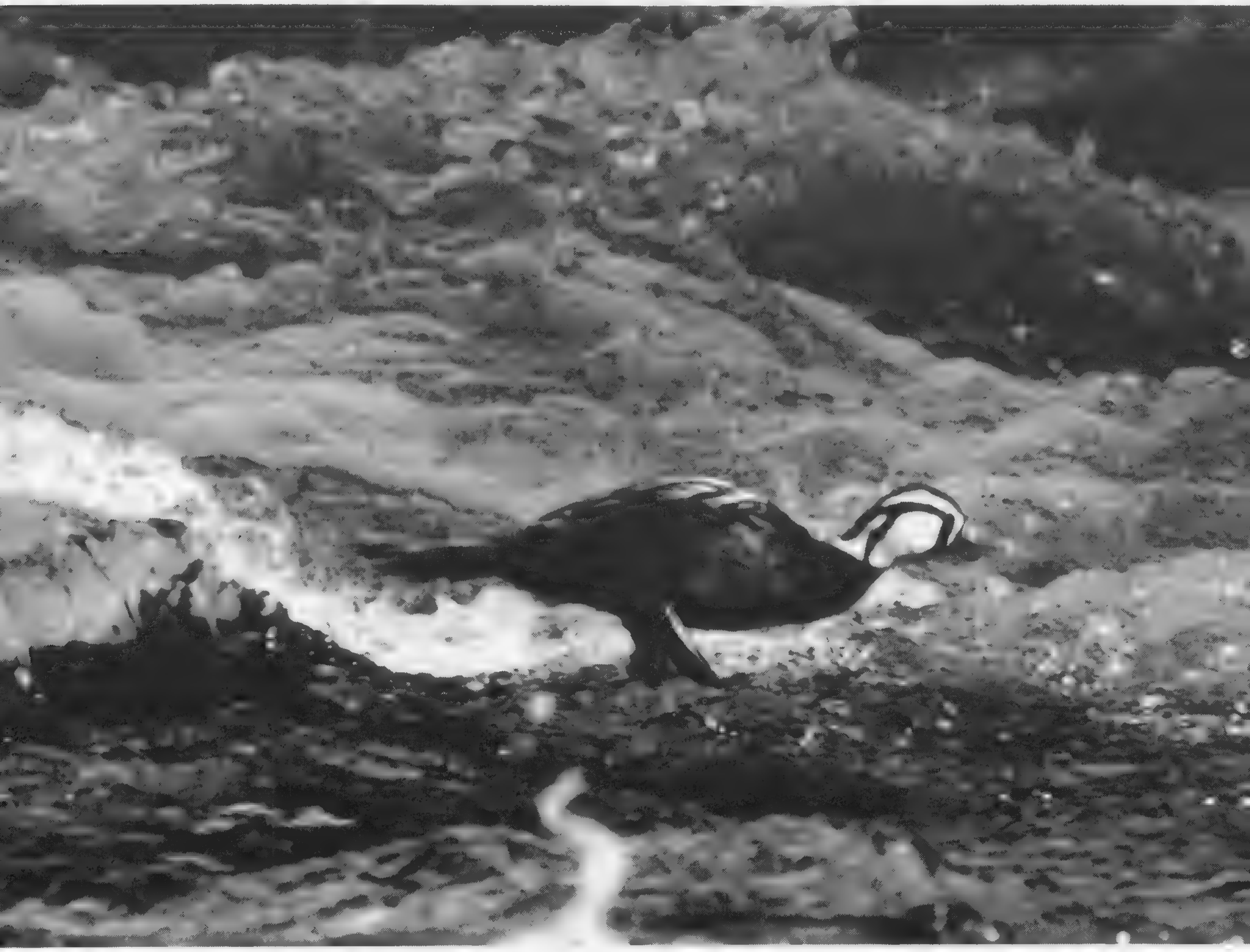


Figure 4. From his perch on a rock, a male Torrent Duck enters the water with a leap. By contrast, the mate of this bird always eased herself into the water.

they turned themselves over to the mercy of the river for a free, swift ride home, going down sideways or backward as the currents buffeted and twisted them about, often invisible in the rapids. They stopped with one quick motion of the powerful tail, skittered easily to the side of the stream, and climbed out on a rock. While perched on rocks, the pair usually dozed or preened.

During the first week after my discovery of the nest, I paid frequent visits to it, but never saw a sitting bird. I had the awful feeling that the pair had abandoned it. The nest, only a slight depression in the earth, contained no down and seemed so exposed and vulnerable. Then, seven days after the discovery of the first two eggs, a third egg appeared, but still no down.

Another seven days passed and from my blind I saw her now sitting on the nest with down fluffed out all around her and tail cocked up. I forded the river and waded down by the steep bank, holding on to exposed roots for balance. I was only 20 feet away when she jerked her head up. As I came closer, she got up, stood on the edge of the nest for a while, and then flew into the water and let it carry her downstream to where the male was loafing on a rock in the middle of the river. I inspected the nest and discovered a fourth egg. The female had thus laid her four eggs one week apart and incubation began with the laying of the final egg. It was raining hard and the whirling wind whipped most of the down off the eggs and into some briars nearby.

Territorial Behavior

The territory of this pair of Torrent Ducks consisted of a stretch of river with its boulders and adjacent banks. Border incidents with another pair downstream occurred frequently. The territorial behavior involved a display in which the male stood in an erect and stiff posture, stretched his neck with the bill pointed upward, and pumped his head up and down. This display was followed by several bows. The bow consisted of lowering the front part of the body, raising the rear, and cocking the head and tail. Males held the deep bow briefly and then assumed the erect posture. The birds performed in a like manner in the water as well.

The first time I watched this behavior, the pair stood on a rock in the stream. All at once the male started pumping and bowing; the female did not. Then another male appeared, climbed up on the same rock, and both males performed facing each other (Figures 5 and 6). After more bows the three went into the water and, from a distance, it appeared that they were fighting. The female disappeared. On the rock again the two males head-pumped continuously, both facing diagonally across the river and calling to each other in a soft plaintive *wheek,* quite unlike the bold assertive note the male delivered when he flew past me. After 20 minutes, the intensity of their display gradually subsided, and the intruding male jumped into the water and floated off downstream. The remaining male continued to call, bowed several times, and then flew upstream where I found him later foraging with his mate.

The second time I observed a territorial encounter I noted another display both on the rock and in the water. This is a "mule kick," a high-intensity bow accompanied by kicking the feet out behind them. I watched the mule-kick activity on the rock and the two feet actually did leave the ground. The activity in the river that I first mistook for a fight was simply the mule-kick display done in the water. On the second observation of the boundary dispute, the female floated downstream and joined the two males on their rock and bowed and called with them. This was the first time I heard a female Torrent Duck's call—a single-syllabic call, somewhat like the male's but lower in frequency and quite hoarse.

These border incidents took place two or three times a week, almost always in the afternoon and always at the same place in the river. Usually they involved only three birds but sometimes there was another female with them. The territorial boundary appeared to be well defined. I never saw either pair feed on the other's side of the boulder on which they displayed.

To test the fidelity of the pair to the territory and its boundary, I waited one day until they were very close to the downstream border of their territory. Then I walked into the stream and waded slowly along the bank toward them. I was between them and their nesting area upstream; behind them lay the territory of another male. When I was about 50 feet from the pair, the male flew off upstream, uttering a declamatory *wheek*. The female stayed behind. As I continued to approach, she showed anxiety and head-pumped continually. She had three alternatives: fly upstream, go to the opposite bank, or float down past the border into another's territory. She went to the opposite bank and began swimming up the stream. At that moment six cows came lumbering down to her side of the river, presenting too formidable an obstacle for the duck. She swam back and climbed upon the rock in the middle of the stream close to the border.

Again I approached her; again she jumped into the river; and, just as she did, the male came whizzing past my ear and made a belly landing right next to his mate. They swam around and around, trapped by the cows on one side, me on the other, and the territorial boundary behind them. For the second time the male flew in what appeared to be an attempt to lead me away. I continued my approach and, when I was about 15 feet from the female, she flew off upstream—and, to my amazement, flew very badly. Even though spurred on by fear, she could hardly get off the water. She flew only about 30 feet and then plopped back into the river where she was now free of danger. I had, meanwhile, found out that each pair remains faithful to a particular stretch of river and respects the well-defined boundary between territories.

Even though any landing on the surface of the water or boulders of another's territory was an infringement, it was all right for a Torrent Duck to fly *through* another's territory. The territorial male chased, or flew with, other males which entered his territory. Often two males, separated by no more than a couple of body lengths, flew low, following the bends of the river. They moved in perfect unison, dipping their wings and altering their course as if under a single control. Usually I did not see them coming because Torrent Ducks fly only from five to, at the most, 20 feet above the surface of the water and their bodies blend in with the background. They streaked past me and disappeared. Often they came back down the river again. Sometimes they splashed into the water together, mounted a rock, and performed the repertoire of bows and mule kicks. The intruding male always broke off the performance first and floated off down the river, out of the other's territory.

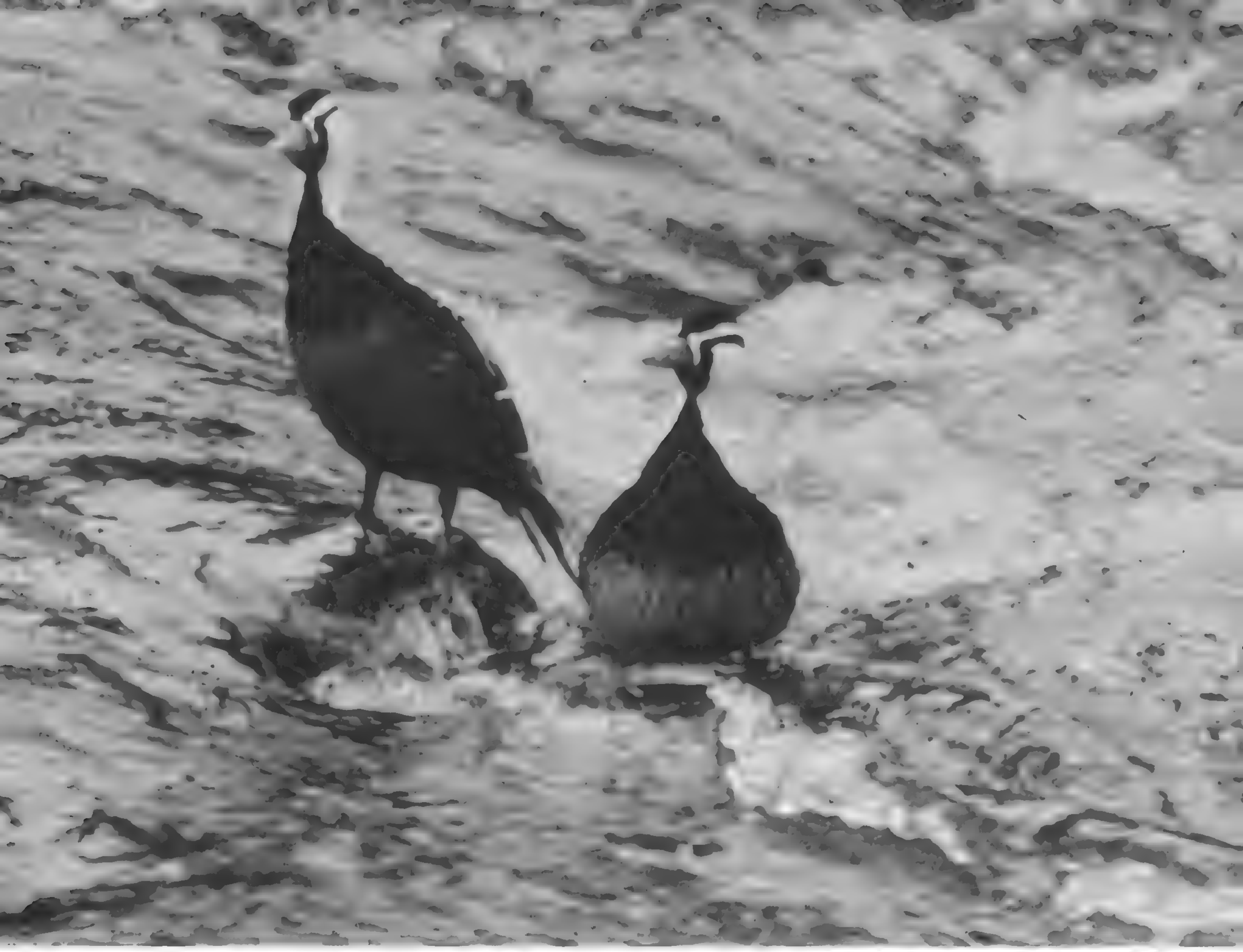


Figure 5 (*above*) and Figure 6 (*below*). Two males standing on boulders that mark their territorial boundaries. Males commonly face each other and display, standing in an erect posture and pumping the head up and down, finally bowing several times.

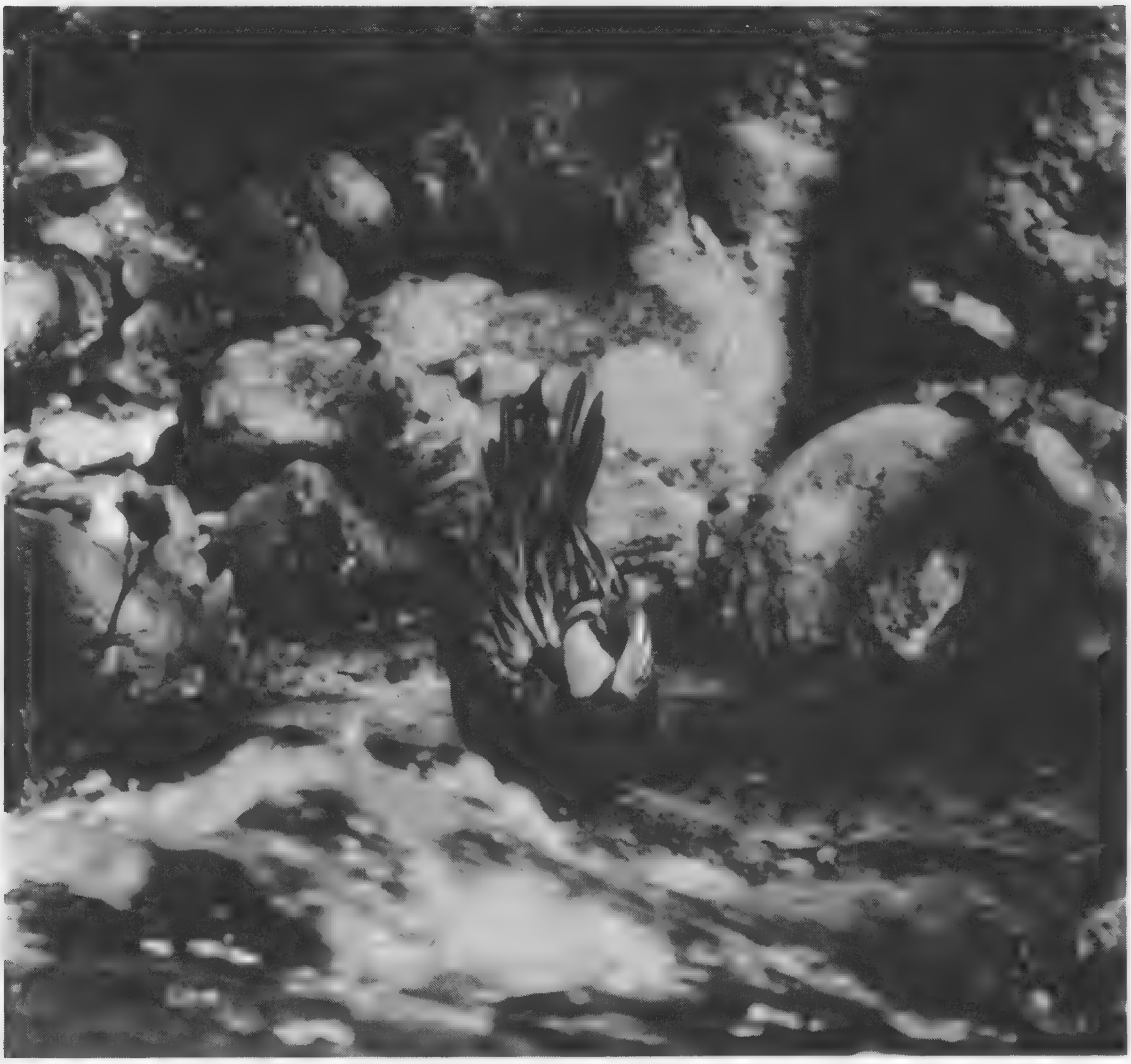


Figure 7. A female returns to the nest only in the male's presence. This male stood on a rock near the nest and bowed and called until the female joined him and made her flight to the nest.

Distraction Behavior

The territorial male used several methods in what appeared to be attempts to elude me and to lead me away from his mate's nesting area. The most common method was to fly swiftly out of the area in a direction that would lead him past me, calling as he flew and thus getting the maximum attention. One of his favorite stratagems was to fly off upstream and then come back downstream underwater. Many times I followed the male upstream only to find, after searching for an hour, that he was feeding placidly in the area whence he had flown.

Another stratagem, a variation of the above, was to jump off a rock and head upstream underwater. Since Torrent Ducks never stay underwater very long, I would watch for his head to bob up not far from where he had submerged, only to find it was a ruse—he had let himself be carried 50 yards downstream underwater.

Nesting Behavior

After the fourth egg arrived, the female spent all of her time either incubating or foraging in the river. The male did not incubate. Each morning, after first light, I usually found the female sitting on the nest. But she soon left, first rising and then making a full circle of the nest as she poked the down about her eggs. This was rather a futile task because as soon as she left the nest, the wind funneling up the river scattered the down off the eggs onto the briars. Each day, when I checked the eggs, I found them uncovered and the briars around the nest full of down.

The female, upon leaving the nest, wasted no time. She fed in earnest for about two to three hours in the morning and for about the same time in the afternoon. The male's feeding habits, on the other hand, were irregular and desultory.

The male was rarely around when his mate flew off the nest, but they soon met for he usually foraged upstream and periodically floated down the river to the nest area. They then remained together until she returned to the nest. The female's foraging dives averaged 12 seconds; she spent about half as much time on the surface between each dive. She sometimes kept this pace up for half an hour before getting out on a rock. There she preened or just stood, but never slept. The male always remained nearby on a rock.

The male's movements were abrupt and positive, including the act of going to sleep. With a quick motion he turned his head over his right shoulder, sometimes closing his eyes, sometimes keeping them open. He often slept standing on one foot with his tail canted to one side for balance. When he was not sleeping, he spent a lot of time preening.

Behavior When Returning to Nest

Near the end of her inattentive period, the female usually fed a while longer in the nest area while the male remained nearby. The female's nest was, as I have said, about nine feet directly above the river. A flat rock, right next to the bank and slightly upriver from the nest, was the scene of the nest-returning activities.

Female Torrent Ducks do not return to the nest unless the male is present. After the female had foraged for a short while in the nest area, the male swam over to the flat rock and hopped up onto it. He began to call and bow (Figure 7). He usually bowed facing away from the bank, but sometimes he bowed in the direction of the nest. The female ignored him for a while, but eventually joined him on the rock. She spent several minutes there, usually looking up toward the nest and pumping her head. All the while the male continued with his bows and calls. If the female happened to get out on the rock so that the male was between her and the bank, the male slipped into the water and swam around her, thus allowing her a clear flight path to the nest. She never gained the nest in one shot. When at last she made the effort, she flew first to an exposed tree root and perched there hesitantly while her mate called intensively from below. Then she half flew and half scrambled to another branch or ledge before finally gaining the lip of the nest.

There were times when her attempts failed and she fluttered back into the river. The male then remained quietly on the rock while she foraged. After a short time, he began calling and bowing again, and they repeated the whole process until she attained her goal. At the nest she paused momentarily before settling down on the four eggs. She went through the motions of placing the down around the margin of the nest, but it was mostly a ritual, for there was little down about. The male remained on the rock below the nest sometimes for as long as an hour. His calling and bowing continued, gradually subsiding in frequency and intensity. Eventually he went off to forage or to perch on another rock for a time.

I observed another behavior of unknown significance yet fascinating. The male, seldom nearby when the female flew down from her nest, invariably showed up within half an hour. If she was resting on a rock, he almost always climbed on the same rock and paused a moment beside her before one or the other of them jumped into the river. This sequence of activity happened so often that I felt it was some form of recognition or greeting. At other times the opposite occurred, the female clambering up on a rock where the male was resting and pausing before one or both of them returned to the water.

While waiting for this female's eggs to hatch, I sought other Torrent Ducks and nests farther downstream. Although I spent most of the next several weeks observing another pair with two young, I periodically checked the nest with four eggs. Actually, the events in the two nests rather paralleled each other (see Appendix), but, in order not to interrupt the sequence of the first nest, I shall continue with my discussion of it and reserve the second nest until later.

Hatching

The female, after 38 days of incubation, still sat on the eggs. However, on 5 November, one of the eggs was pipped. On 7 November, two days later, the pipping had not progressed.

On 8 November, in the afternoon, I found the parents foraging and immediately inspected the nest. Three of the eggs had not begun to pip; the hole was much bigger in the pipped egg. I saw the duckling move, faintly.

On 9 November, the opening in the pipped egg was no larger, but the chick inside was active—breathing. Moreover, two other eggs were pipped.

On 10 November, all four eggs were pipped. Of the weather that day, I wrote: "Rain followed by snow near blizzard proportions, followed by sunshine, then more rain, then sun and rain – all in the space of 45 minutes. Typical Andean weather!"

On 12 November, one week after the first egg had begun to pip, I checked the nest at 10:09 and discovered three downy chicks (Figure 8). A fourth was still in the egg. After 43 to 44 days, there they were, fuzzy gray ducklings. They were a sleepy looking bunch. Their eyes were closed most of the time and they moved about very little.

Incubation had lasted 43–44 days. If this nest was typical of Torrent Ducks, the species has a longer incubation period than has been recorded for any other species of the Anatidae.

I kept the nest under observation all day. The female remained with her brood until 19:05 when she finally flew down to the river. Twenty-five minutes later she returned. In the intervening time, I checked the nest and found four chicks. My record reads: "Very windy. Spitting rain. I crossed the river with great difficulty. The water is rising—up two inches since this morning."

On 13 November, the river raged. It was higher than at any time during my stay along El Ternero and flowed at 7.8 feet per second. In the early morning the female remained on the nest. She left at 09:05. The chicks stayed in the nest but were active. They moved around, climbed over each other, preened, stood up, stretched their wings, but never ventured beyond the cup of the nest.

Within an hour the female returned to the nest. At 11:25 the chicks wandered off the nest rim. During the afternoon the female made several forays to the river below. The young, however, stayed in the nest, except for one that was accidentally shoved out. He managed to scramble back again.

On 14 November, early in the morning—before 06:30—I found the parents and three chicks on a rock below the nest. The fourth chick was missing and may have been swept away by the current. The others clambered over the rocks and took their first foraging swims.

Locating Another Nest

Meanwhile I had been looking downstream in a deep, narrow gorge where I had previously seen a pair of Torrent Ducks. I was sure there was a nest. To find a nest by searching tree cavities in that somber gorge seemed a difficult and unpromising way to go about it, so I stationed myself in a blind on the edge of the cliff above the gorge, hoping that the ducks would lead me to it. After a week or so, I saw a male climb out on a huge boulder and make a couple of bows. The female soon appeared. This first sighting soon led to the discovery of their nest 60 feet above the water in a crevice in the cliff. This was a real cliff, all rock straight down, so high and steep that the female had to stop five times before reaching her nest while her mate called energetically from below.

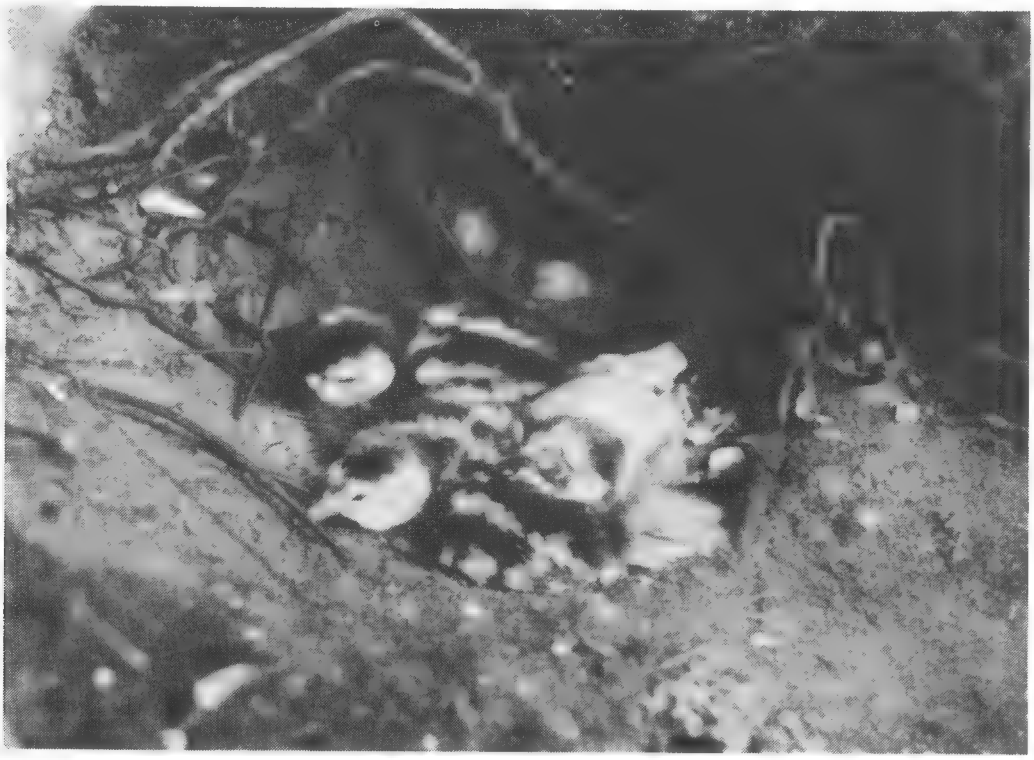


Figure 8. A nest with three downy chicks on 12 November, one week after the first egg had begun to pip. This nest was situated nine feet directly above the water.

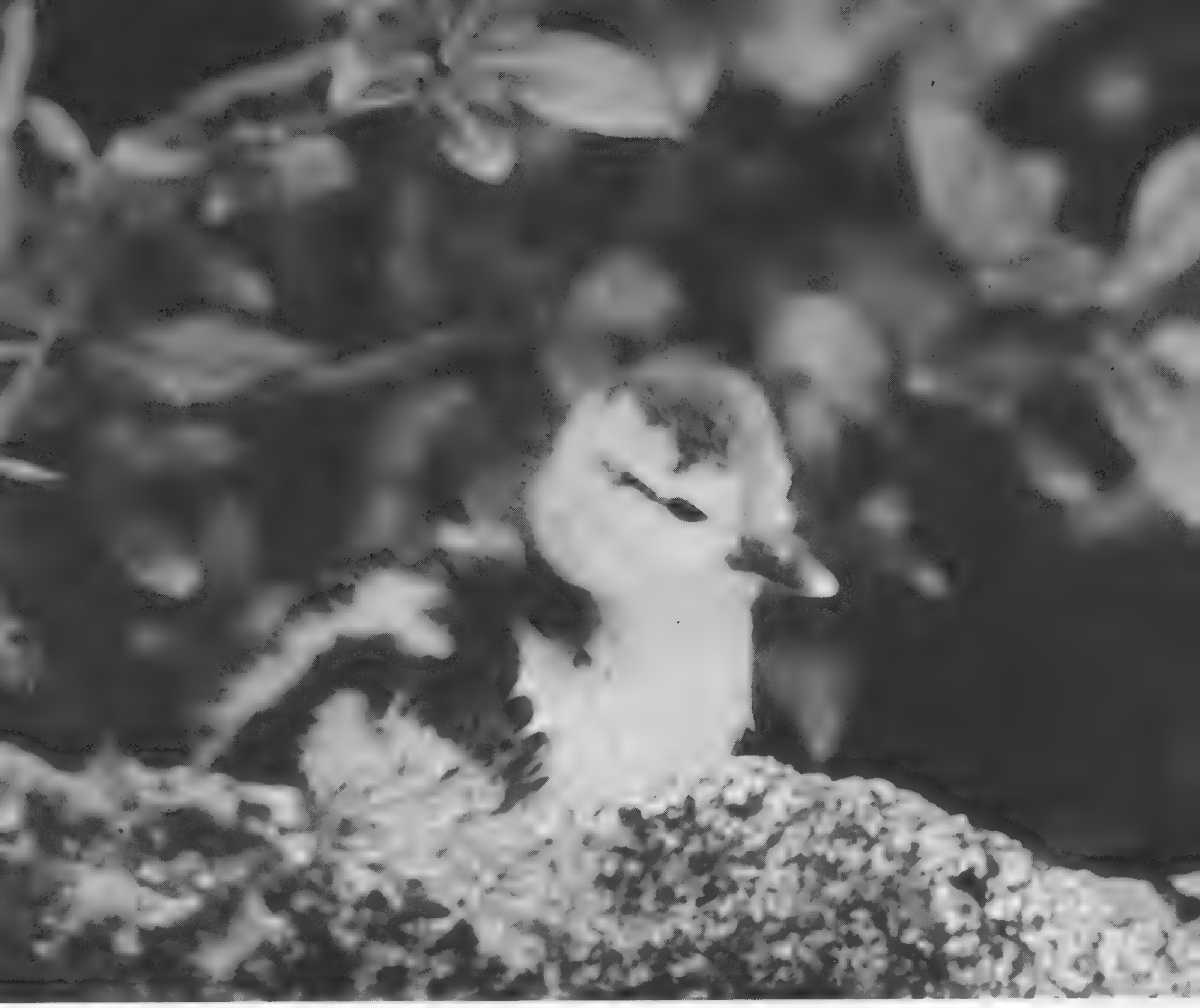


Figure 9. A young Torrent Duck sits near the water's edge four hours after tumbling from its nest 60 feet above the water in the crevice of a cliff.

With this second pair I observed the same courtship bows, the same nest-return behavior, and heard the same calls. I was unable to determine the contents of their nest because the top of the cliff overhung it, hiding it completely from above.

Behavior on Departing from Nest

During the next days I sat in my blind on the cliff edge across the gorge from the nest site and kept a camera trained on the crevice. One day, the female appeared at the entrance to the crevice. She was in shadow, silhouetted against the sunlit face of the cliff behind her. I was photographing her when, to my astonishment, a duckling appeared on the ground glass beside her. A duckling, gray with a dark eyestreak, looking all fluffy and alert (Figure 9). Then out popped another ball of gray fluff. They all stood there together for several minutes. There should be two more, I thought. No more came.

Then the female flew off the ledge, fluttered down to the river, and swam about in a back eddy pool behind a boulder. As she swam, she called vigorously and continuously to the two ducklings that were standing on the ledge 60 feet above her. They made head thrusting movements just as the adults did.

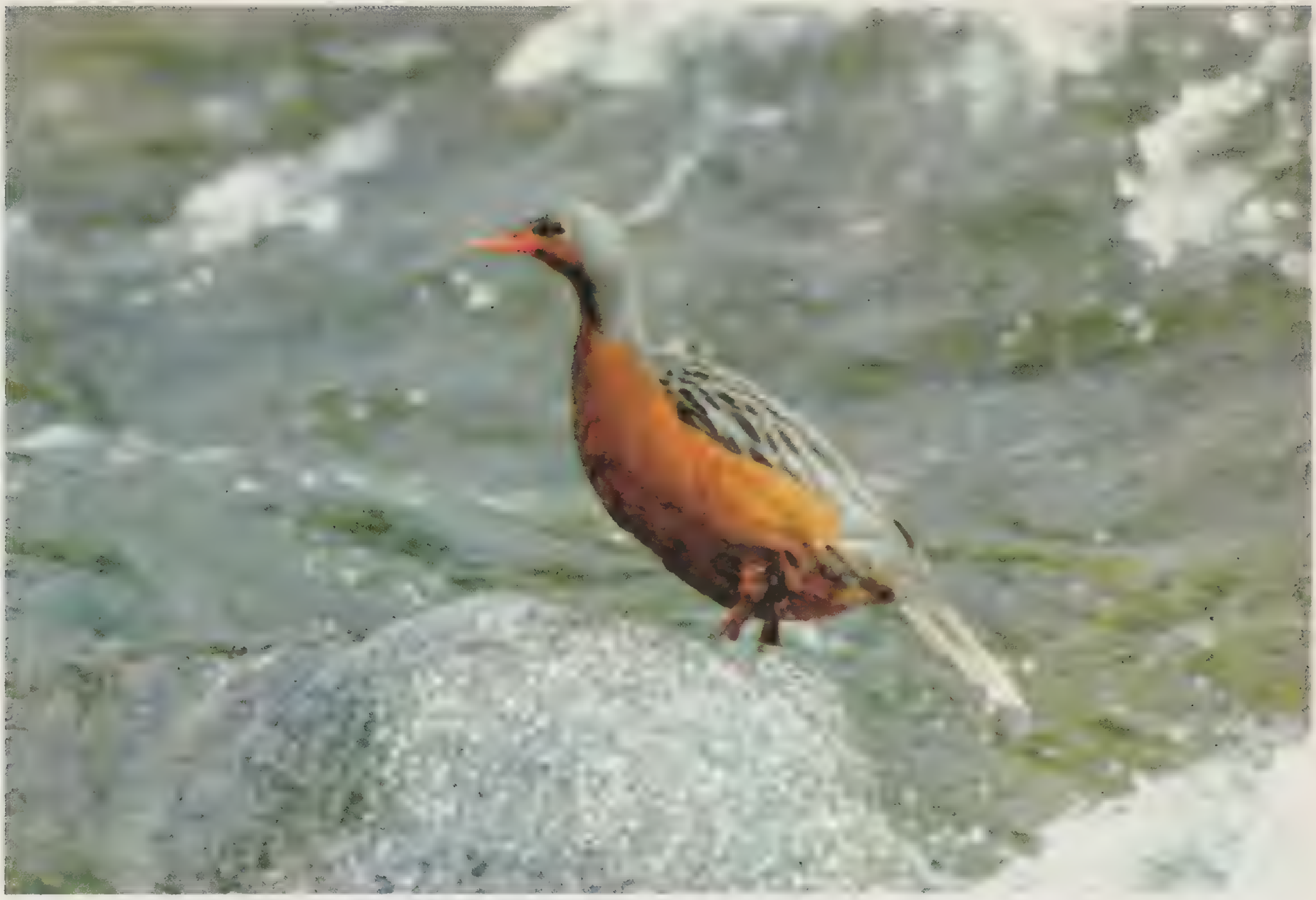
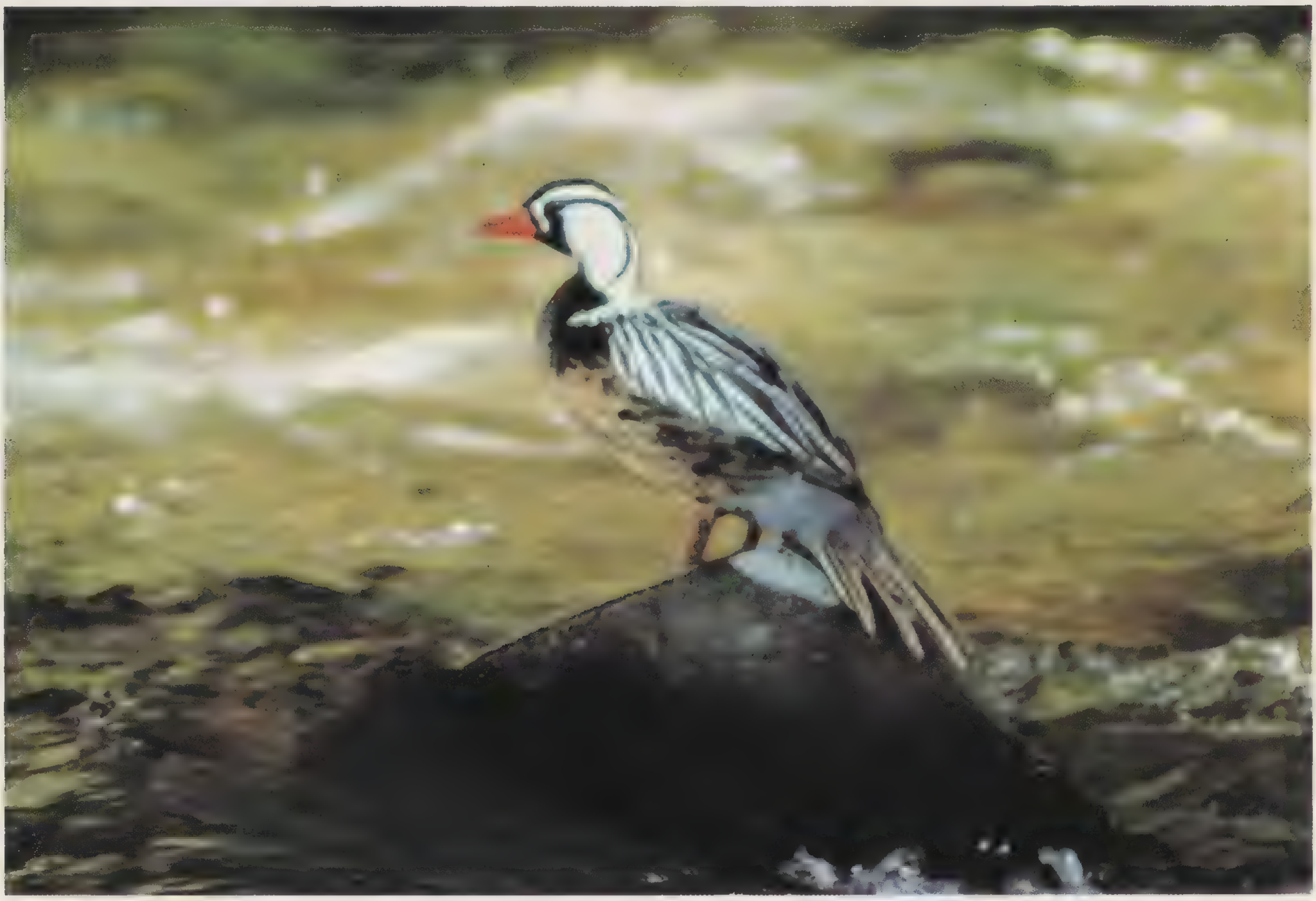


Plate II. The brown and gray colors of the female Torrent Duck *(above)* contrast sharply with the striking black and white of the male *(below)*.



The first one out of the nest made the first leap into the torrent. Only a matter of 30 seconds or so after the parent started calling from the river, the duckling toppled off the edge and, tumbling as it fell, bounced off a projection of the cliff, and then onto bare jagged rocks and stony debris at the base. It appeared on the stones at the edge of the pool where its mother was swimming, looking completely unperturbed by its hair-raising (for me) entrance into the world.

Without a moment's pause it went into the water and swam around easily in the eddy which revolved in a slow whirlpool behind the boulder. Almost immediately it made forays into the faster water of the river and had no difficulty getting back to the calmer water of the pool despite the buffeting it took in the turbulence at the edge of the river. It also dipped its head under to feed.

About two minutes after the fall of the first chick, the second, responding to the insistent calling of its parent, took the plunge. It, too, bounced and crashed onto the rocks at the base of the cliff and disappeared from view in a thicket of thorns and briars. Somehow, its plunge seemed more perilous than that of the first chick, and, because it did not appear for some time, I thought it had met its end. Eventually it showed up at the water's edge and, without hesitation, joined its sibling in the river.

This drop to the river was not as perilous as it first appeared. A Torrent Duck chick has very little weight for volume—very little density. A duckling just out of the egg weighs 1.25 ounces, and that miniscule weight is wrapped up in a ball of fluffy down. As the chick goes hurtling through the air, it does not pick up much speed. Actually the down slows its speed, as do the feathers on a shuttlecock, and also cushions its landing.

Locomotion and Feeding Behavior of Young

The downy chicks floated high on the water. Though at the mercy of the currents, it was soon obvious that they were masters of the art of propulsion and navigation in a torrent and showed to what a remarkable degree the species is adapted to its highly specialized environment (Figures 10 and 11).

In all the length of the El Ternero that I knew, this particular spot was the wildest, narrowest, and most rapid part of the river. The water was all white with turbulence and rapids, sluices and waterfalls, whirlpooling currents, and tumbling waves. If torrents were to be their natural element for life, their initiation was immediate and severe.

The male had been upstream and now appeared. With the second chick in the water the female no longer called continuously nor did she look up at the nest, so I knew that no more ducklings would issue forth. The parents, however, called at frequent intervals. Almost immediately they started escorting the chicks into faster water, yet usually preventing the chicks from getting too far out into the river by keeping them between themselves and the bank. Right off the chicks were able to do two maneuvers I often watched in adults: "skate" over the water against the current to make headway; and, when the current was too strong to overcome by direct assault, maneuver across it on the diagonal.

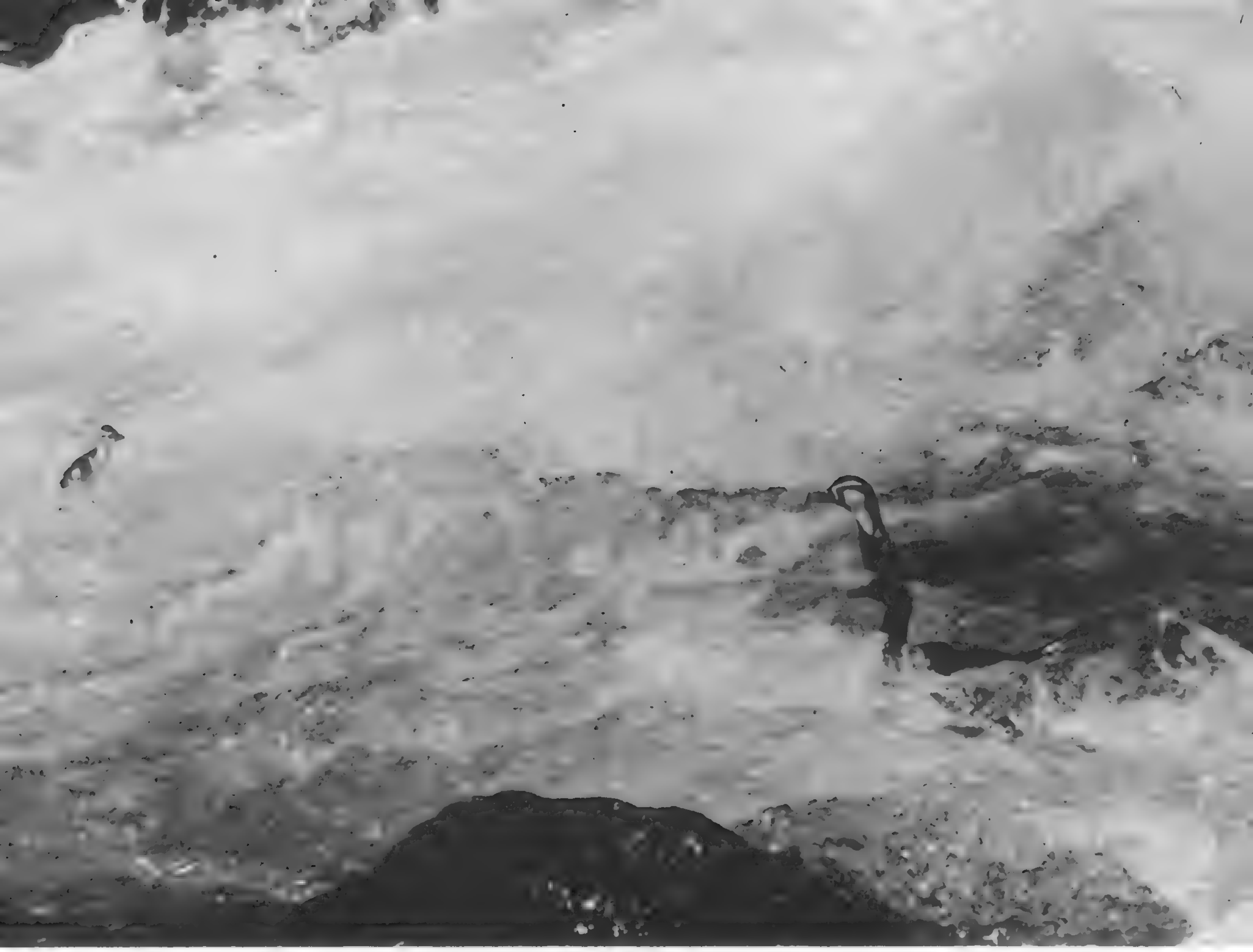
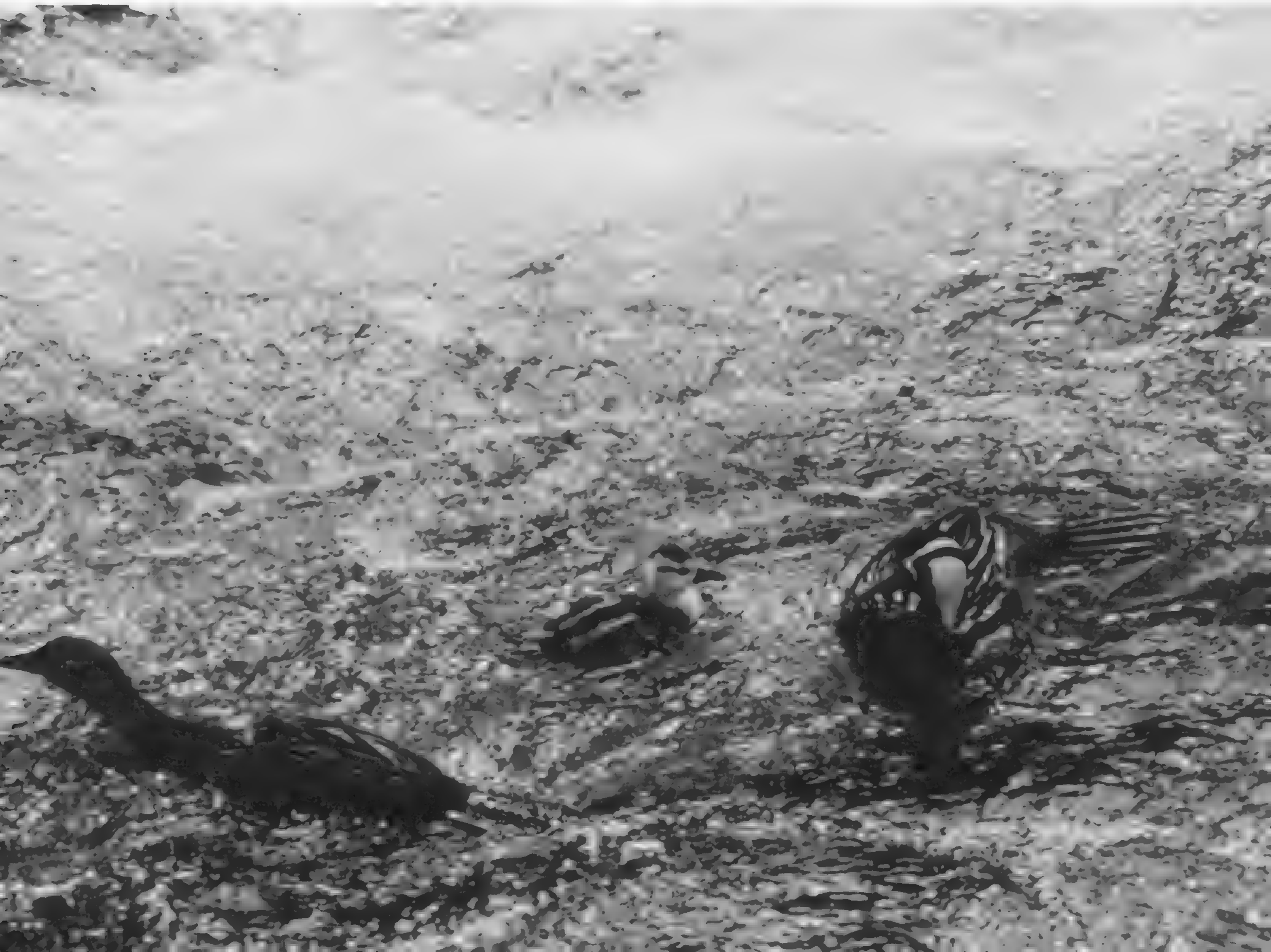


Figure 10 (*above*) and Figure 11 (*below*). This Torrent Duck chick swims with its parents in the rapids of the El Ternero. It floats high in the water and navigates well in the strong currents, although it has been in its new environment for only two hours.



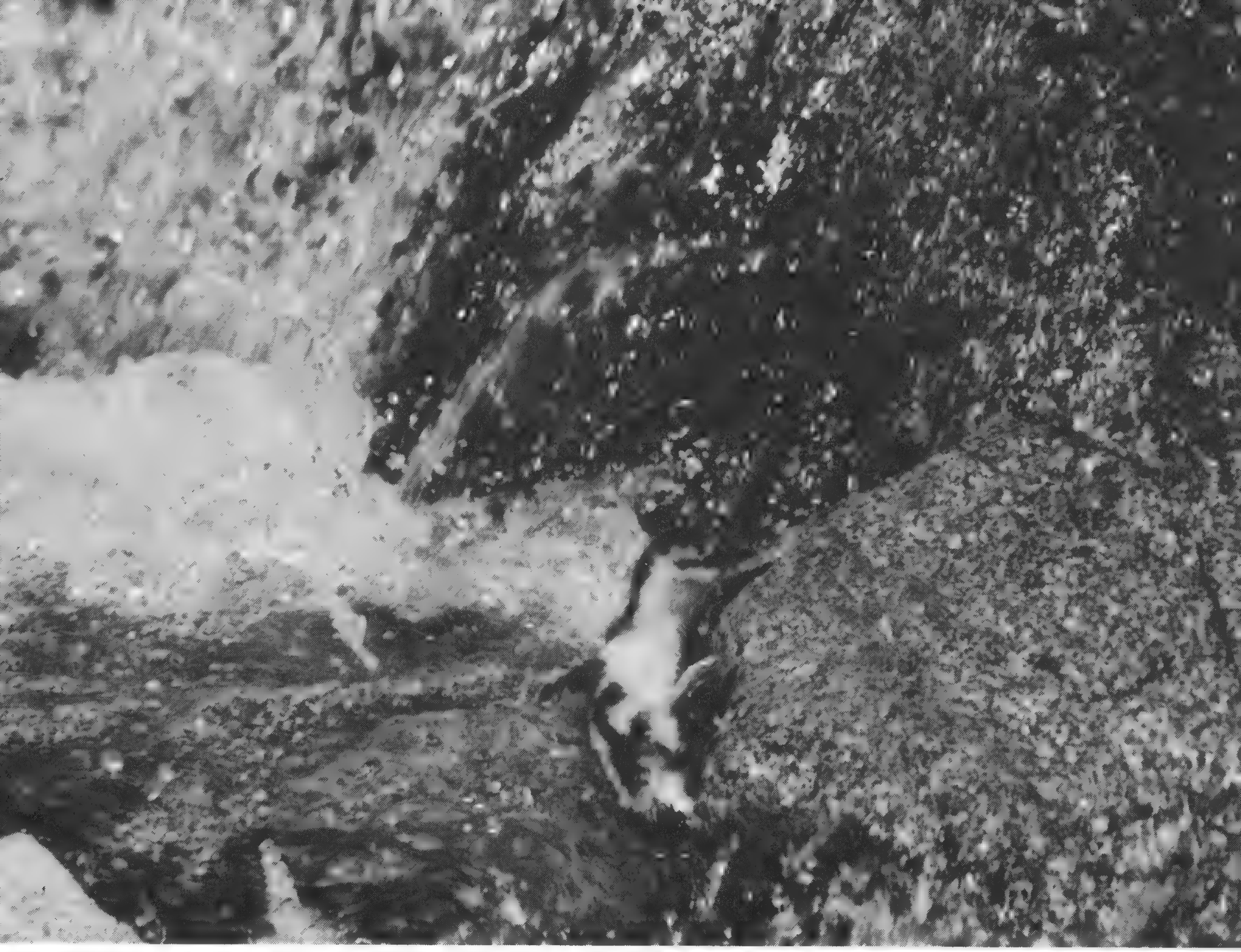


Figure 12. A Torrent Duck chick tries to climb a rock. It uses its wings to maintain balance, and beats them vigorously to assist the climb. It seldom remained on the rock for long, but usually plunged right back into the water.

They also started climbing rocks, but with some difficulty (Figure 12). They used their wings for balance, and beat them vigorously to assist the upward climb. They succeeded in most of their rock-climbing attempts. Climbing rocks represented an important part of their early learning, for it meant rest and refuge from the rigors and exertions of swimming in a torrent. Once on the top of a rock the chicks plunged right back into the water unless the rock was a particularly high one. Even then, they hesitated only for a short time.

Hating to leave them, yet desiring to cross to the other side of the river to watch them close at hand, I walked upstream for an hour before I found a place to ford the river. Another hour brought me to the pool where the two ducklings had taken their initial swim. As I approached, I heard the male and female calling loudly and soon discovered the reason—one chick was missing. It had obviously been swept downstream. I watched as the parents started to slide downstream. And then I saw it, the missing chick, on a high rock in the middle of the river downstream. It was head-pumping and calling frantically.

The parents swam to a back eddy on the opposite side of the river near the rock on which the downy was marooned, calling continuously. The duckling responded by jumping into the torrent and skittering across the top of the water toward the parents. Then, in close company, the three worked their way up along the edge of the river, judiciously using the eddies and counter currents until they arrived opposite the pool where the other duckling was swimming about. The male and female, trying to get their errant chick back to the pool, alternately crossed the stream and called, thereby demonstrating the technique and direction for crossing. The duckling started across but the current was too strong for it and the swift water drew it downstream to the rock from where it had started. It climbed back on the rock and began calling again. The parents moved down and repeated their calls. Once again the chick jumped into the water. This time the current swept it away, around the bend of the river and out of sight. In a moment, the parents eased themselves into the current and allowed themselves to be swept in pursuit of their duckling, leaving the other chick in the pool upstream.

I walked around the bend and found the duckling swimming in a pool by the edge of the cliff, occasionally ducking its head into the water for food, and always making forays into the fast water. Then it climbed out of the pool and generally poked around, looking things over, curious and alert, unperturbed. Although it showed no fear of me as I approached with my camera, it managed to keep a certain distance between us by continually moving and jumping into the water and swimming about.

After taking a few pictures, I climbed up a grassy bank. It was getting late. I looked back for the chick and it was gone. Then I caught sight of the parents on a rock in the stream opposite the point where the chick had been. And although I had not seen the chick return to the parents, a small gray form with a black striped head popping out from beneath the female's feathers indicated that it had successfully made the trip across the stream.

Soon the three were in the water slowly working their way back up the stream along the bank. Finally they reached a rock opposite the pool where all this time the other duckling had been busy dunking its head underwater for food. The parents swam across to the pool, called to the chick they had retrieved, and crossed back and forth several times between the pool and the chick. Finally, the chick headed out across the river. The little duckling skittered across and seemed to ride, not on the water, but on the froth that hissed on top of it. The duckling reached the other side quite easily and the entire family was together.

They were together, but all was not over for the day. The parents then proceeded to lead their chicks out of the wildest part of the river to calmer waters upstream. At one point, where they encountered a waterfall and also a stretch of fast water running between steep banks with no eddies for safe havens, they climbed rocks along the bank as the only recourse. At another point they confronted tumbled rocks 15 feet high. The parents stood on top of the pile and called while the ducklings worked their way up. For every two rocks they climbed they fell back one. Several times one of them—the weaker, probably the chick that had been swept downstream—nearly reached the top only to fall all the way to the bottom again, bouncing off rock after rock and ending up in every position but upright, but always unscathed. By the time darkness fell, they had made it to smoother sailing and I lost them from view on the opposite side of the river.

On 1 November, I returned to the gorge area and spent the day with this pair and their two ducklings. Most of the time the male stood guard on a rock usually a bit upstream from where the family group happened to be feeding.

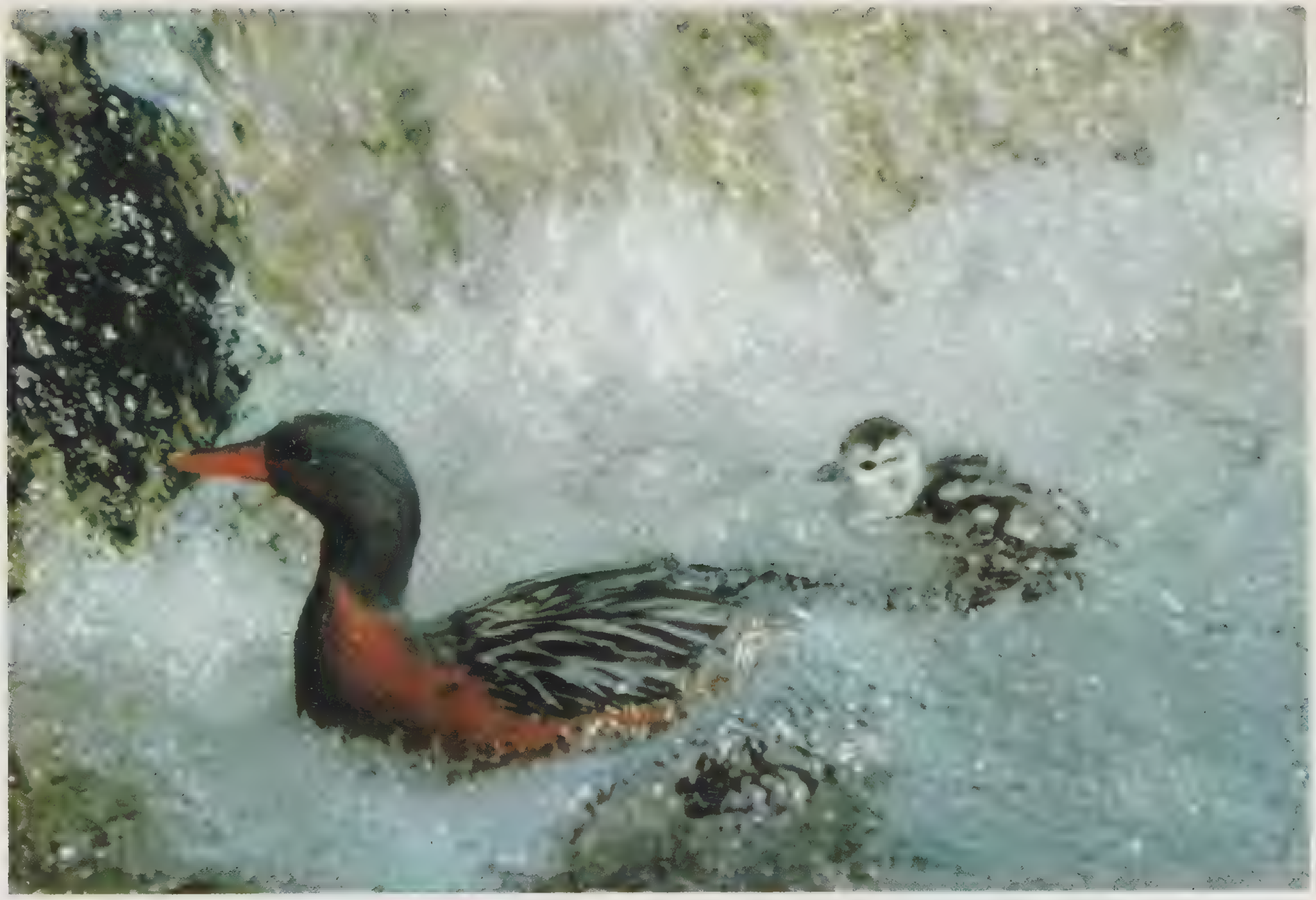
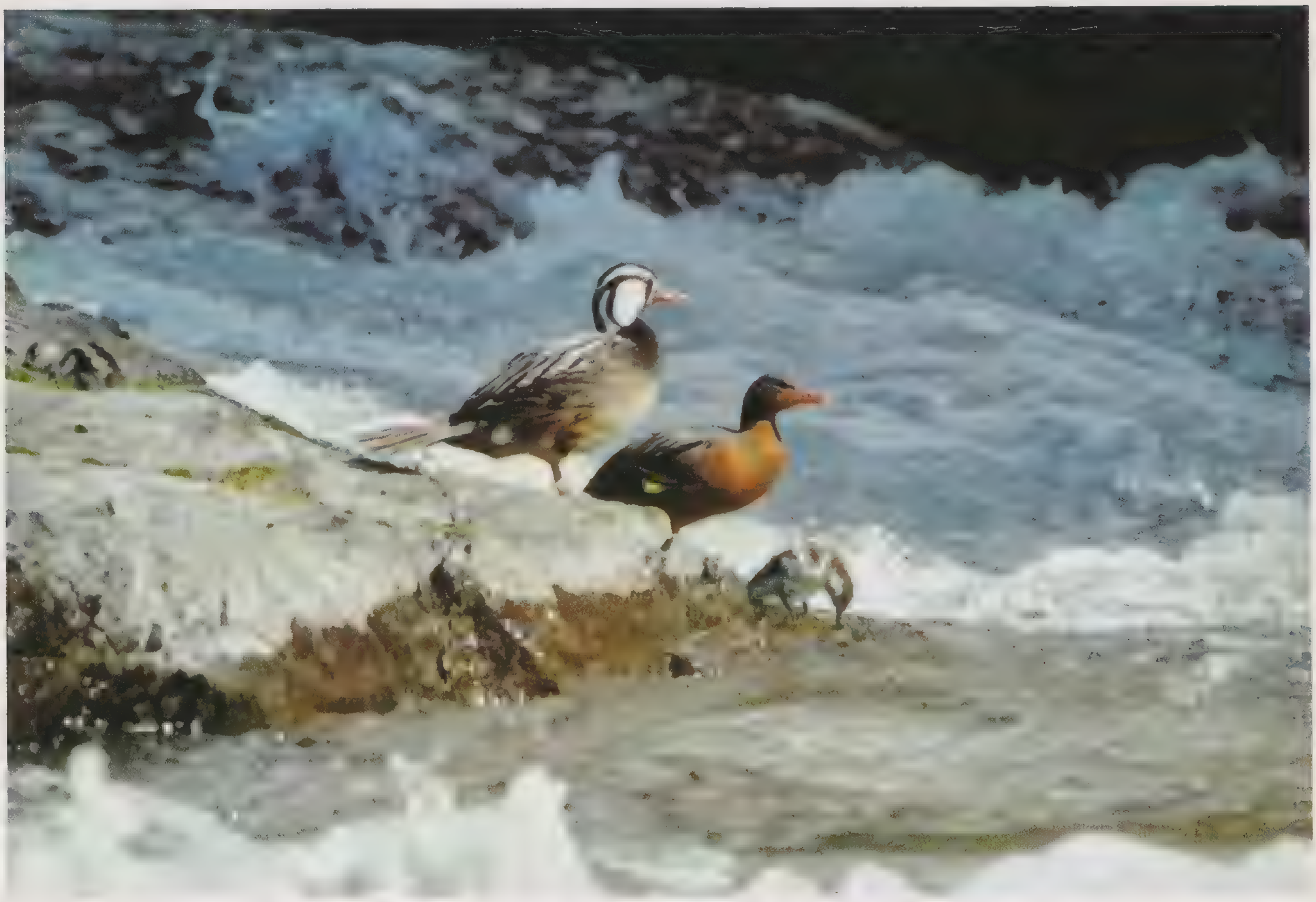


Plate III. *Above,* a young Torrent Duck with its female parent.
Below, two chicks forage under the watchful eyes of the parents.



The downy young fed most of the time in the shallows along the edge of the river. The female remained in constant attendance, either feeding or swimming alongside of them. The ducklings fed with their heads underwater and they attempted to dive—to get beneath the water. They upended and kicked wildly with their oversized feet, but, due to their buoyancy, they either failed to submerge entirely or, if they did submerge, they popped up immediately like corks. By the end of the day the chicks had foraged a total of 6 hours and 28 minutes in five periods with an average of one hour and 18 minutes per period. The longest foraging period was one hour and 42 minutes; the shortest, 55 minutes. They had rested or been brooded for a total of 2 hours and 33 minutes. Although they foraged and rested along a half-mile stretch of river, they spent most of the day along 300 yards of El Ternero.

On the sixth day of waterborne life I discovered that one of the ducklings had disappeared in the night. Since I know of no predators on Torrent Ducks except man, I assume that it was swept downstream. The remaining duckling dived quite regularly now, going to the bottom and staying as long as just under six seconds at a time. As it grew older, it spent much more time resting on rocks and much less time foraging.

Meanwhile, Marvin Cecil had collected 18 Torrent Duck eggs from five nests and, using a portable incubator, had transported them by jeep, jet, and motor car safely back to Florida. Seventeen of the eggs hatched. Unfortunately, the ducklings all died.

I have limited my discussion in this paper entirely to Torrent Ducks, their nests and various behaviors, and have done so, I might add, with difficulty. The area was alive with other birds. I often spent a day on the farm of a friend of mine, by a lake filled with waterfowl. I saw coots struggling to rise off the water and Ashy-headed Geese (*Chloephaga rubidiceps*) circling about. There were Ruddy Ducks (*Oxyura jamaicensis*) and grebes, and Brown Pintails (*Anas georgica*) all over the place, and more ibises than I had ever seen before. I found a White-throated Tree Runner (*Pygarrhichas albogularis*) busily pecking away at its hole in a tree, and two Southern Lapwings (*Belonopterus cayennensis*) calling incessantly and drinking at the same time. I listened to the haunting whistle of the Chiloe Widgeon (*Anas sibilatrix*) and watched the Yellow-headed Caracaras (*Milvago chimango*) ride the thermals. One of the greatest thrills occurred when I came upon two ducks grazing on a grassy bank beside the El Ternero. I thought they were widgeons until the late afternoon sun suddenly flashed on the iridescence of a pinkish speculum. They were a pair of Bronze-winged Ducks (*Anas specularis*) and as I approached, they barked, like dogs. All these other birds were very fascinating, yet not fascinating enough to keep me very long from the Torrent Ducks on the El Ternero.

Summary

This paper describes a study of the Torrent Duck (*Merganetta armata*), undertaken in Rio Negro Province of Argentina from September to November 1968. The birds, about whose natural history little has been recorded, live in rapid mountain streams of the Andes, where they feed almost exclusively upon the larvae of stoneflies (*Rheophila*). Their adaptations to life in these

rapid currents include a torpedo-shaped body, proportionally large feet, a long, stiff tail, and a narrow, flexible bill. They generally work upstream on feeding forays, and frequently remain underwater for 16 seconds or more. One female's foraging dives averaged 12 seconds. Upstream locomotion on the water includes skittering across the surface using their tail as a sculling oar and their feet as paddles. They tend also to move upstream along the banks where the current is not as swift, and effectively use the reverse eddies and still waters behind boulders. I found two nests, one in a cavity formed by the roots of a *Nothofagus* tree along the bank nine feet above water, the other in a crevice in a cliff 60 feet above the water. I kept the two pairs under close surveillance. The species is monogamous. Pairs maintained rather strict territories that encompassed about 0.6 mile of river for a pair, although most of their time was spent in a one-third-mile stretch of river. Territorial behavior consisted of calls, bowing displays, and "mule kicks" both in the water and on boulders. The female generally left the nest for several hours in the morning and several more in the late afternoon. The male did not incubate, but remained in the territory and usually in attendance with the female when off the nest. One week separated the laying of the last three eggs in one nest. In both pairs the male displayed to entice the female to return to her nest. The incubation period of one of the nests was 43 to 44 days. In one of the two nests, the two chicks that hatched jumped to the water sixty feet below, landing on rocks on the bank. Both, unharmed, plunged into the water and began swimming with the parents.

Acknowledgments

I wish to thank Mr. Joel Kuperberg, formerly Manager of the Caribbean Gardens, Naples, Florida, and Dr. Manley L. Boss, Chairman of the Department of Biological Sciences, Florida Atlantic University, Boca Raton, for the organization of this trip. In the field, I am especially grateful for the assistance of Mr. Marvin Cecil, formerly Curator of Birds at the Caribbean Gardens, who had his own work to do yet found time to help and advise me. Also of great help were Sr. Andor Kovacs and his four sons of El Bolson, Argentina; Sr. Jorge Politis of Buenos Aires; Sr. Luis Ruiz and family, who owned the farm bordering the El Ternero River; and Sr. Drago Milinkovic, whose lumber mill near the river we used as headquarters.

APPENDIX

Chronology of Two Nests of Torrent Ducks

NEST I

Sept. 3–10	Observed pair and mapped territory.
Sept. 10	Set up blind.
Sept. 16	Found nest with two eggs, no down.
Sept. 23	Third egg in nest, no down.
Sept. 30	Fourth egg in nest, lots of down.
Nov. 5	Egg pipped.
Nov. 7	No progress in pipped egg.
Nov. 8	Hole in pipped egg larger, duckling moved, faintly.
Nov. 9	Hole no larger, duckling more active. Two other eggs pipped.
Nov. 10	All eggs pipped.
Nov. 11	No change.
Nov. 12	Three downy chicks out by 10:09; one very active in egg. Chicks quiet. Four hatched at 19:05.
Nov. 13	Chicks in nest all morning. More active and outside nest in afternoon, but back by night.
Nov. 14	Parents and chicks all on rock below nest by 06:30.

NEST II

Oct. 13	Discovered nest in crevice in cliff, 60 feet above river.
Oct. 29	Female and two downy chicks in crevice. Female flew to river; chicks dropped down, landed on rocks, and went to water.
Nov. 1	Male on guard on rock; downy young and female feeding or resting. Stayed most of day along 300 yards of river.
Nov. 4	Adults and one chick in usual place. Other chick missing.

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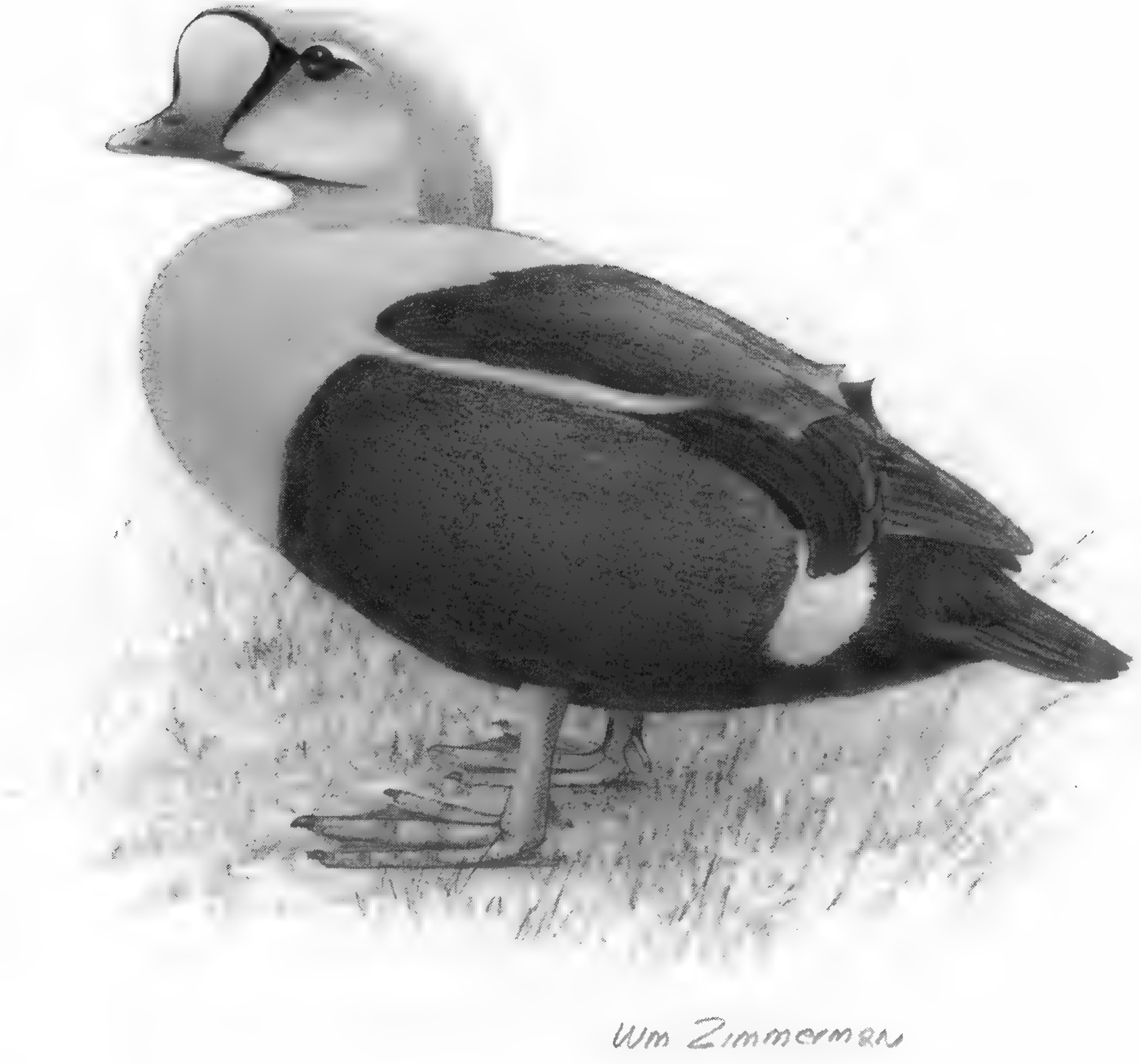
CHAPPAQUIDDICK ISLAND, EDGARTOWN, MASSACHUSETTS



King Eider, *Somateria spectabilis*. Drawing by William Zimmerman.

DISPLAYS OF FOUR SPECIES OF BLUE-WINGED DUCKS

FRANK MCKINNEY

Photographs by the author

Following the lead of Delacour and Mayr (1945) and Lorenz (1953), most comparative studies of waterfowl behavior have been concerned with the use of courtship displays as indicators of taxonomic relationships. These investigations, summarized by Johnsgard (1965) who has been the leading worker in this field, have produced inventories of display repertoires for most members of the family Anatidae—the ducks, geese, and swans. This information on the distribution of homologous displays—i.e., displays having a common origin—together with a comparison of anatomical characters (see Woolfenden, 1961) is sufficiently detailed to permit confident conclusions on the relationships of almost all species, and very few unusual or "aberrant" forms remain to intrigue the taxonomist. With the realization of this goal, comparative behavior studies on waterfowl can now progress a stage further with the search for factors which have been responsible for the evolution of specific differences, a field as yet scarcely touched.

Within the group of dabbling ducks (tribe Anatini), for example, the diversity of display repertoires is complex, many species having 25 or more distinct movements and calls. Some of these behavior patterns are widely distributed in the tribe; others are apparently unique to one species. Some displays are frequent in one species, rare in another. There are specific variations in the degree of ritualization of many movements, in the order of displays linked in sequences, and in the degree of elaboration of plumage features reinforcing signal movements. While we have noted these differences in many species, we understand very little about the factors that have produced them.

The blue-winged ducks comprise one of the best defined groups within the Anatini, all seven species having diagnostic blue patches on the upper wing coverts. Four species, Northern Shoveler (*Anas clypeata*), Cape Shoveler (*A. smithi*), Red Shoveler (*A. platalea*), and Australian and New Zealand Shovelers (*A. rhynchotis*), have large spatulate bills specialized for straining plankton from the water surface. The other three species, Blue-winged Teal (*A. discors*), Cinnamon Teal (*A. cyanoptera*), and Garganey (*A. querquedula*), have small bills. The broad features of the ecology and behavior of several members of the group are known, but there are no detailed studies of the displays.

My aim in this paper is to describe and compare the display movements and calls of four species—the Northern Shoveler, Blue-winged Teal, Cinnamon Teal, and Cape Shoveler. By drawing attention to homologous behavior patterns, differences between species, and the characteristics of the communication system, I will try to identify some factors that have influenced the evolution of displays in the blue-winged ducks.

Study Birds

I observed wild Northern Shovelers and Blue-winged Teal from 1958 to 1962 at Delta, Manitoba, Canada, and established captive flocks of Northern Shovelers (about 60 birds in two winters) and Blue-winged Teal (about 30 birds in three winters). Most of the captives were raised from eggs, collected on the Delta Marsh. My study of Cinnamon Teal, from 1960 to 1962, was based entirely on 12 wild birds, captured mostly as juveniles in the fall of 1960 in Utah and transported to Delta, and their progeny.

From October to late April, we kept the ducks inside the hatchery building where cement ponds provided swimming water. On most winter days, the temperature inside the building was around 40°F. During the rest of the year, we kept the birds in outdoor pens and encouraged small numbers of full-winged ducks to breed under fairly natural conditions in a large flight pen (see McKinney, 1967). Some Northern Shovelers and Blue-winged Teal that were feather-clipped and held in pens without wire tops, attracted many wild males that I observed at close range.

Forty-eight individually marked Northern Shovelers, raised in captivity, were watched after release to the wild at Delta in May 1960, and 38 in May 1961. I also made some observations on marked Blue-winged Teal, released by Charles W. Dane in the spring of 1962, and studied wintering birds of both species at the Rockefeller Refuge in Louisiana for one week in mid-March 1960.

During three springs, 1965–1967, I had further opportunities to study full-winged Northern Shovelers breeding in large flight pens at the University of Minnesota's Cedar Creek Natural History Area, 30 miles north of Minneapolis (McKinney, 1967).

While on a 10-week visit to South Africa in July and August 1968, I observed Cape Shovelers—a pre-breeding group including about 20 pairs and five unpaired males—at Little Brak River, near Mossel Bay, Cape Province, from 16 to 26 July, and a dense breeding population at the sewage farm at Paarl from 9 to 19 August. I watched captive Cape Shovelers, in the Jonkershoek waterfowl collection of the Cape Department of Nature Conservation, at close range. Earlier, between 1949 and 1954, I had become familiar with this species at The Wildfowl Trust, Slimbridge.

In summary, I know the Blue-winged Teal, Northern Shoveler, and Cape Shoveler, both in the wild and in captivity. My information on the Cape Shoveler's annual cycle of behavior is incomplete because I made most of my observations on the pre-breeding and early nesting stages. The Cinnamon Teal I know only from captives breeding in flight pens.

Terminology

Moynihan (1955:20) defined "a display" as a behavior pattern which is ritualized: "A behavior pattern will be considered ritualized if there is evidence that it has signal function and that it has become specialized in adaption to that function." In distinguishing "displays" from other behavior patterns, I have used the indirect kinds of evidence currently employed by ethologists. There is no experimental proof of the signal functions.

I have followed Moynihan's convention of capitalizing ritualized behavior patterns and taken many names for displays from Lorenz (1953). Some of his terms are admirably descriptive (e.g., Decrescendo Call); others, such as Inciting and Repulsion, imply the birds' intentions or the functions of the displays. While the former descriptive terms are preferable, I continue to use the latter as convenient "labels" for these widely recognized displays.

Annual Cycle in North American Species

The Northern Shoveler, Blue-winged Teal, and Cinnamon Teal breeding in North America perform regular migrations (see Phillips, 1923, for ranges and schedules). Pair-formation occurs on the wintering grounds. Mr. Robert H. Chabreck tells me that, in Louisiana, Blue-winged Teal form pairs between late October and December, and Shovelers begin in mid-December and continue until they depart for the breeding grounds. Captive Northern Shovelers at Delta followed a schedule similar to that of the Louisiana birds, but the Blue-winged Teal and Cinnamon Teal showed little activity until January and February. Female Shovelers and Blue-winged Teal are paired on arrival at Delta in April; the populations of both species have a surplus of unpaired males which continue to try to obtain mates throughout May.

Adult female Northern Shovelers and Blue-winged Teal "home" to nest in the same area as in previous years (Sowls, 1955). Each pair restricts its movements to a relatively small area, and paired males are aggressive toward members of the same species (Hochbaum, 1944). In the Blue-winged Teal (Sowls, 1955; Dzubin, 1955; Evans and Black, 1956) and Cinnamon Teal (R. I. Smith, 1955), strict territorial boundaries are hard to define and the "home ranges" of neighboring pairs overlap to some extent. There is much less overlap of Shoveler home ranges. Sowls noted that the Northern Shoveler was the "most territorial" of the dabbling ducks he studied and my observations confirm his. Although the males of all three species are very aggressive, Shovelers establish the most clearly defined territories.

From May to August, egg-laying, incubation, and brood-rearing occupy the females. The pair-bond is strong, often lasting until late in the incubation period or even for a short time after hatching (see references *in* McKinney, 1965a). If the first clutch is lost, females will renest one or more times (Sowls, 1955) and, in most cases, the pair-bond is probably still intact and re-pairing is unnecessary.

When pair-bonds finally break, usually in late June, the males gather in flocks. By this time, they have begun to assume the eclipse plumage, molting the flight feathers in July-August. The females become flightless later than males—after the brood has been raised.

Male Blue-winged Teal and Cinnamon Teal assume the breeding plumage between September and December. Northern Shovelers are later, the earliest not being in full plumage until November or December. In all three species, adult males molt earlier than first winter birds by at least several weeks, but there is considerable individual variation in the molt schedule. Most Delta captives followed a pattern similar to that of wild Northern Shovelers and Blue-winged Teal in Louisiana (Robert H. Chabreck, *in litt.*).

Annual Cycle in the Cape Shoveler

Avian breeding seasons in South Africa are less clear-cut than in North America and the annual cycle in this species is not yet well understood. Siegfried (1965) summarized the evidence and concluded that, in the southwest Cape, a pronounced breeding peak occurs in spring—July to September—as length of day and temperature increase, following the period of winter rainfall. In the Witwatersrand, where the rainfall comes in summer, broods appear in every month of the year with apparent peaks both in spring and autumn. Siegfried suggested that the unusual situation may arise because of differences in food available for broods in natural and man-made water areas. He believed that breeding is stimulated primarily by environmental conditions created by rainfall.

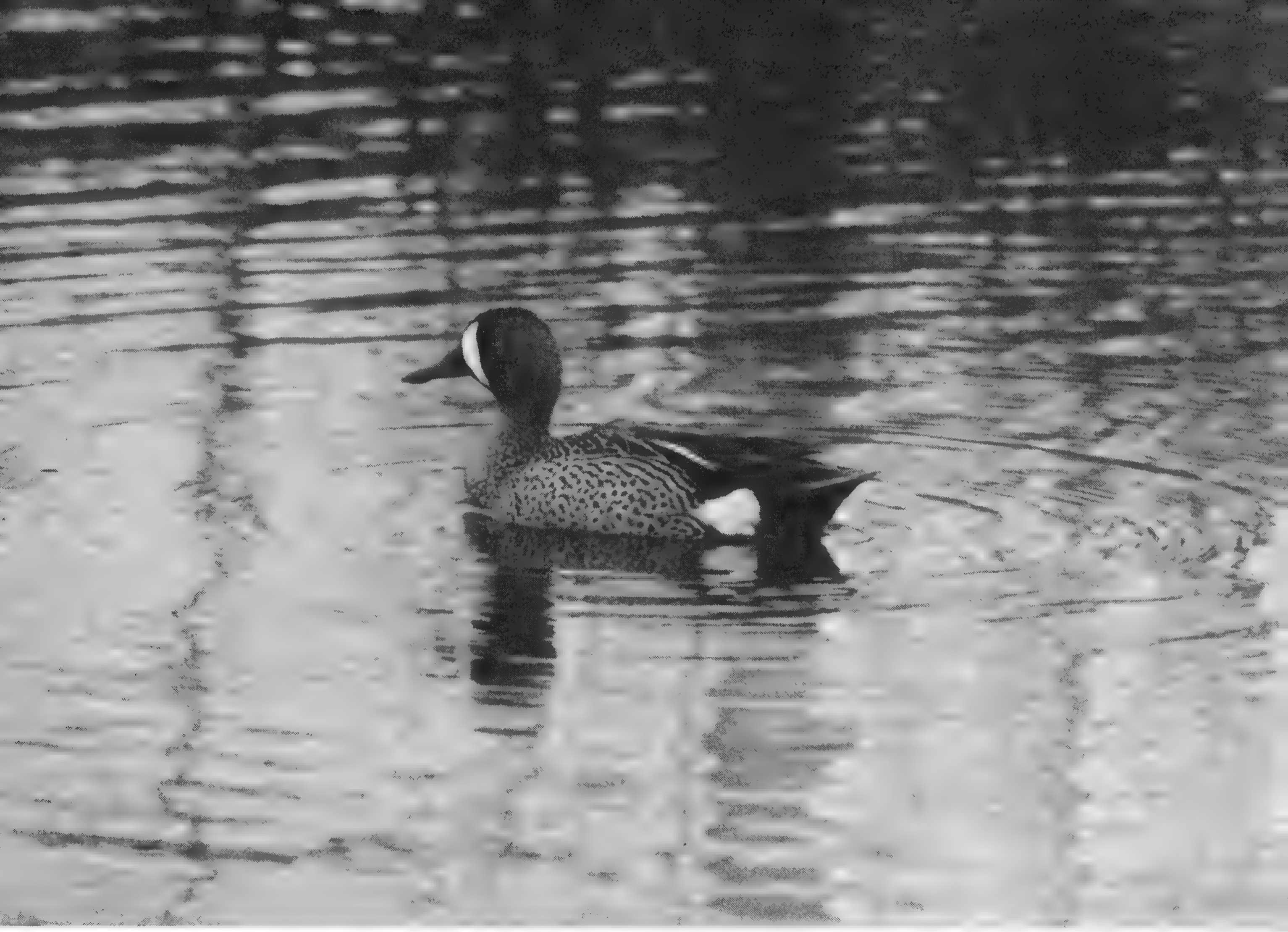


Figure 1. A male Blue-winged Teal giving Repeated Calls, a display associated with pair-formation. The male, holding his body stationary and his head fairly erect, utters a series of from two to 20 clear soft whistles. The vibrations of the bird's body during the previous calls in this series caused the ripples on the water. Repeated Calls are also heard when a pair of Blue-winged Teal is disturbed and flies up quickly.

Although we have little information from banding returns, seasonal movements clearly take place. Siegfried also suggested that true migration, nomadism, and local movements may all be involved, initiated probably by the quality and quantity of available food.

In its general breeding behavior I agree with Siegfried's conclusion that the Cape Shoveler is very like the northern species. Its territories are small and hostility between males is vigorous. The pair-bond is similarly strong, and a number of observations (quoted by Siegfried) of males accompanying females with broods suggest that it persists even longer. Though the wing molt appears to be a typical post-breeding phenomenon, the Cape Shoveler does not assume an eclipse plumage markedly different from its breeding plumage.

Pair-formation

Pairing is gradual in captive Northern Shovelers. Usually those individuals in the most advanced plumage are the first to perform occasional displays, becoming, about the same time, more aggressive toward one another. Both males and females begin to show preferences, orienting their displays repeatedly to certain individuals. But, as Weidmann (1956) found in the Mallard (*Anas platyrhynchos*), the early alliances are unstable and one cannot distinguish firm bonds for sure until pairing activity has been going on for many weeks.

At least by mid-March, most Northern Shovelers and Blue-winged Teal wintering in Louisiana are firmly mated and pairing activity centers around a few females for which the remaining unpaired males compete. These "courting parties," including one female and a group of males, are familiar sights on the Canadian prairies in late April and early May (Hochbaum, 1944). On the water, the males perform a variety of displays and swim persistently after the female. Usually, the group soon takes to the air and a twisting pursuit-flight follows, the males continuing to call as they attempt to keep up with the female. Similar courting flights occur in the Cape Shoveler (Siegfried, 1965; personal observations).

Monogamy seems to be normal in these four species and it is difficult to understand how Millais (1902) and Kortright (1942) came to the conclusion that polyandry is common in the Northern Shoveler. Indeed, the pair-bond is notably strong and long-lasting in this species, and, in my experience, paired males are exceptionally intolerant of other males (McKinney, 1965a, 1967).

Male Displays Primarily Associated with Pair-formation

Repeated Calls.—The male gives a series of single or double notes, typically from a stationary posture with the head held fairly erect (Figure 1). The number of calls in a series varies from two to 20 or more. In all four species, the posture is the same and the calls are evenly spaced, but the notes produced are very different. The Northern Shoveler gives either single or double "tooks": *took-took* . . . *took-took* . . . *took-took* . . . *took-took* or *took* . . . . . . *took* . . . . . . *took* . . . . . . *took*. The two forms frequently intergrade without a

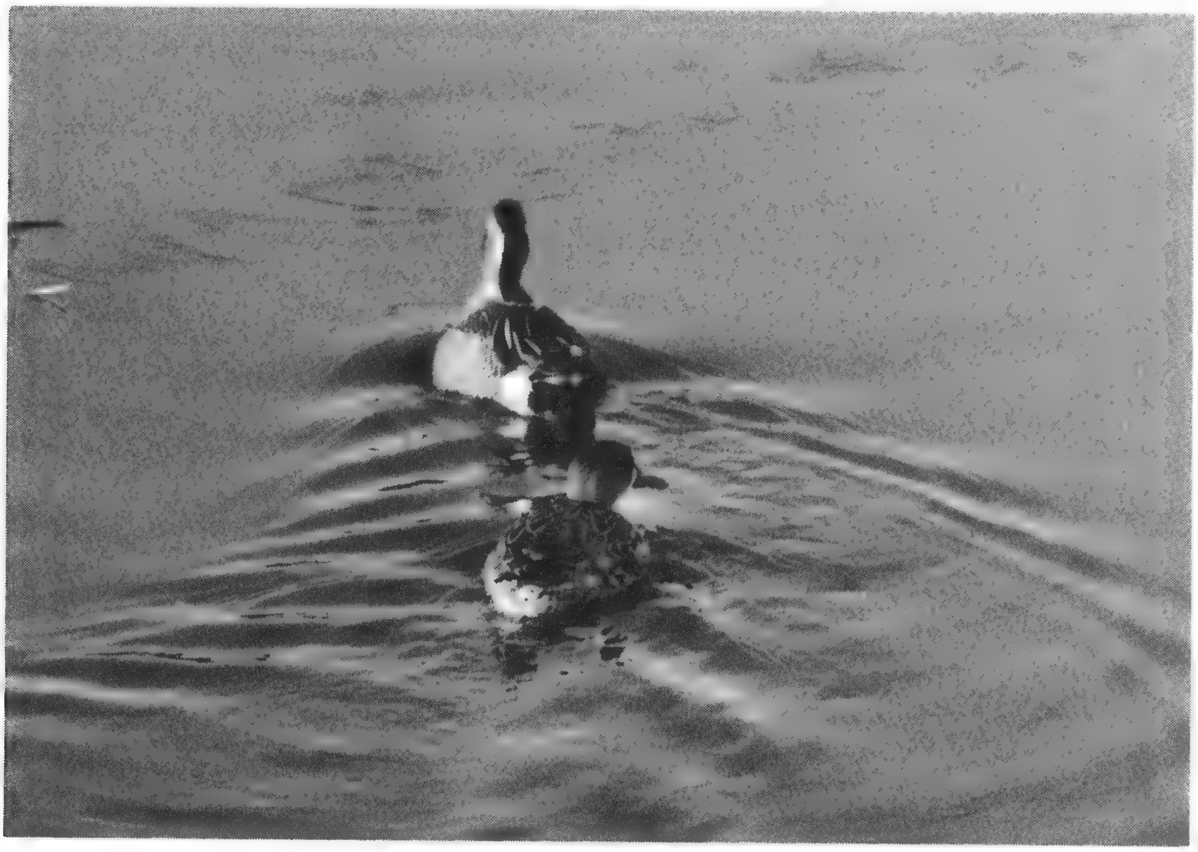


Figure 2. A male Blue-winged Teal performing Turn-back-of-head, a display associated with pair-formation. The male moves in front of the female while she is swimming or walking. He holds his head stiffly, pointing his bill away from her.

pause. Sometimes, at the beginning or end of a series, a quiet, wheezy sound replaces the full notes, but the even rhythm is the same.

Most Blue-winged Teal males give a series of quiet, clear whistles: *pew . . pew . . pew . . pew . . pew*. Some individuals do not seem capable of producing these whistles and their Repeated Calls, as well as their other vocalizations, have a deeper, nasal sound: *pay . . pay . . pay . . pay*.

Repeated Calls—and all other male vocalizations—are much quieter in the Cinnamon Teal than in the above two species, as Wetmore (1920) pointed out for the calls accompanying Hostile Pumping. They are rolling rattles, reminiscent of the calls of the male Garganey: *rrar . . rrar . . rrar . . rrar*. In the Cape Shoveler, the homologous calls are quiet and hoarse with a rising inflection, rendered in my notes as *cawick* or *po-huk*.

The Northern Shoveler gives Repeated Calls from the start of pair-formation until about the time the male deserts his mate—i.e., from December through June. During the pair-formation period, unpaired males give these calls as they remain stationary, either on land or water, usually somewhat apart from other birds. Often there appears to be no external stimulus triggering the calls. At other times, however, they are given as a response to a disturbance, in situations of mild alarm—for example, when I walk into the pen.

Repeated Calls are heard when a pair of Northern Shovelers or Blue-winged Teal is disturbed and flies up; in the Shoveler, Fast Calls (see below) precede Repeated Calls. Paired males of both shoveler species regularly give Repeated Calls as they swim or fly back to the centers of their territories after a dispute with a neighbor. In this situation these male calls probably function in maintaining contact with the mate. On several occasions, I have seen female

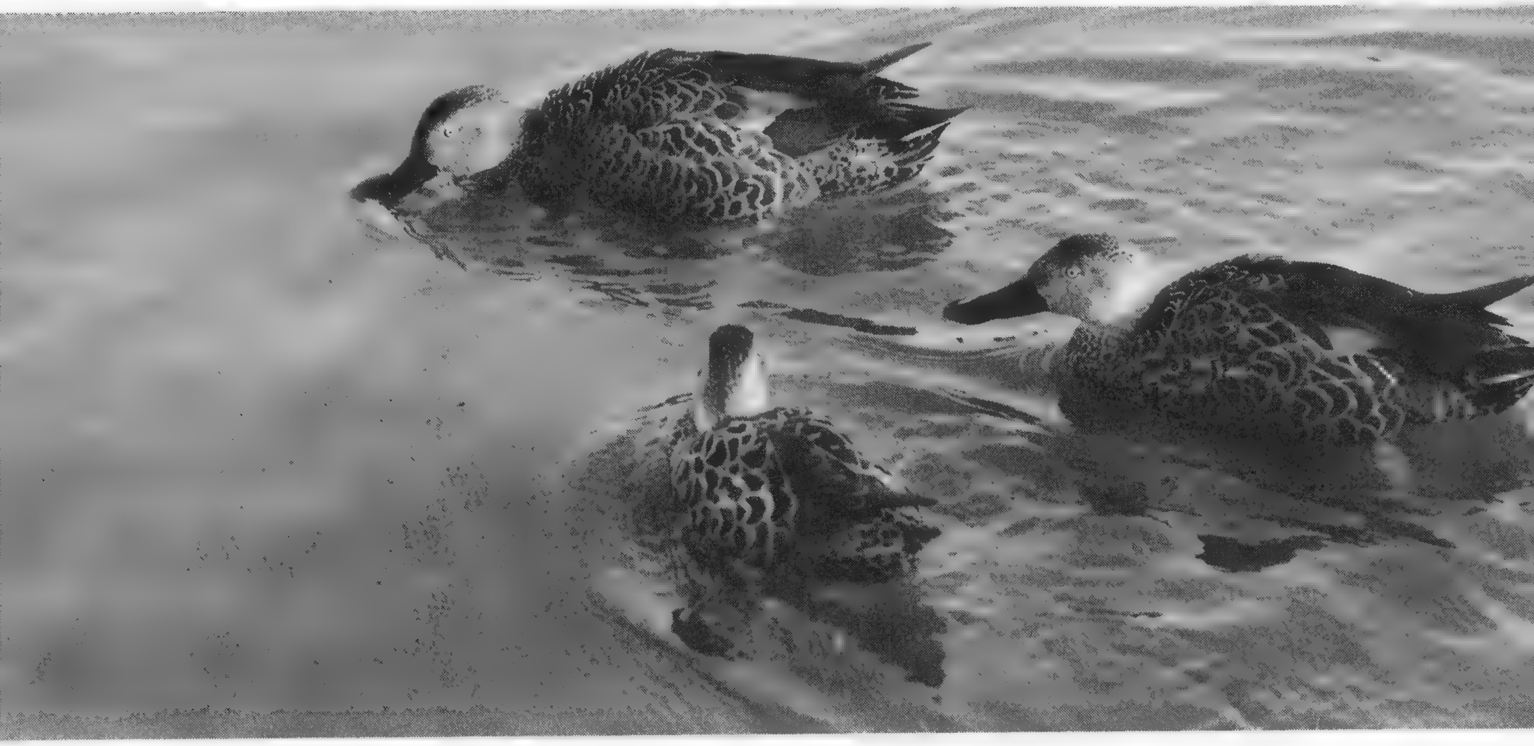


Figure 3. A male Cape Shoveler performing Lateral Dabbling, a display associated with pair-formation. As the female swims toward a male, he turns, keeping his side toward her. If she changes direction, he, too, turns slowly so that she still faces his side. He dips his bill into the water and dabbles on the surface as if feeding. He erects the feathers on his back and flanks and partly exposes the speculum. He paddles rapidly with his feet and holds the posture for several seconds.

Blue-winged Teal and Northern Shovelers respond to Repeated Calls from their mates by moving to join them.

Fast Calls.—Male Northern Shovelers give short bursts of rapidly repeated *took* calls in a variety of situations. During pair-formation season, one hears them especially when two pairs come close together on the water, during Lateral Dabbling (see below) and before a Jump-flight (see below). When a pair is flushed—at least between March and June—the male usually gives a short burst of fast *tooks* as he takes off. Then, after rising perhaps 10 feet, the notes change abruptly to a series of Repeated Calls.

Cape Shovelers have corresponding Fast Calls, a machine-gun-like rattling *rararararara* which they give at times between Repeated Calls. These Fast Calls are very conspicuous before a Jump-flight and during the ascent. I have not detected Fast Calls in the Blue-winged Teal or Cinnamon Teal.

Turn-back-of-head (TBH).—As the female walks or swims, the male moves in front of her, with the long axis of his body at a slight angle to her line of movement; he holds his head stiffly with the bill pointing away from her (Figure 2).

This is one of the commonest displays associated with pair-formation in all four species. In the Northern Shoveler, even when a pair-bond appears to have formed, the male continues to give this display for a period of days or weeks. In cases where the female tolerates or actively accepts the male, he often gives the display while swimming a few inches from her. On the other hand, an unpaired male will approach a paired female and perform TBH in front of her even though he is threatened by the female or her mate. In such a situation, the male may be six to eight feet from the female.

Lateral Dabbling. — This display (Figure 3) was called "Gabbling" by Lorenz (1953), and "Mock Feeding" by Johnsgard (1965). The male aligns his body laterally to the female, dips his bill into the water, and makes a series of dabbling movements as in the familiar pattern of feeding on the surface of the water. The feathers of the flanks and along the center of the back are conspicuously erected, and the speculum is often partly exposed. The bird paddles rapidly with the feet and holds the posture stiffly for several seconds.

Lateral Dabbling commonly occurs when the female swims toward a male in a courting party. If she changes direction, the male slowly adjusts his position so that he remains with his side toward her. The male is usually swimming, but sometimes the display is given by a bird standing at the edge of the water (Figure 4). Lateral Dabbling is sometimes associated with TBH and often given by a paired male while his female is Inciting and threatening another male.

In the Blue-winged Teal and Cinnamon Teal, I have heard no calls accompanying the dabbling movements; but the Northern Shoveler male often gives a series of Fast Calls while the bill is in the water, and Johnsgard (1965) records calls, associated with this display, in the Cape Shoveler.

Heinroth (1911) and many other observers have noted that several shovelers often swim in a circle, each bird dabbling close to the tail of another. Delacour and Mayr (1945) state that the blue-winged ducks "have a peculiar ceremony in which one or several pairs swim around in a circle, head to tail, merry-go-round-like, with the bill immersed and water running through it as

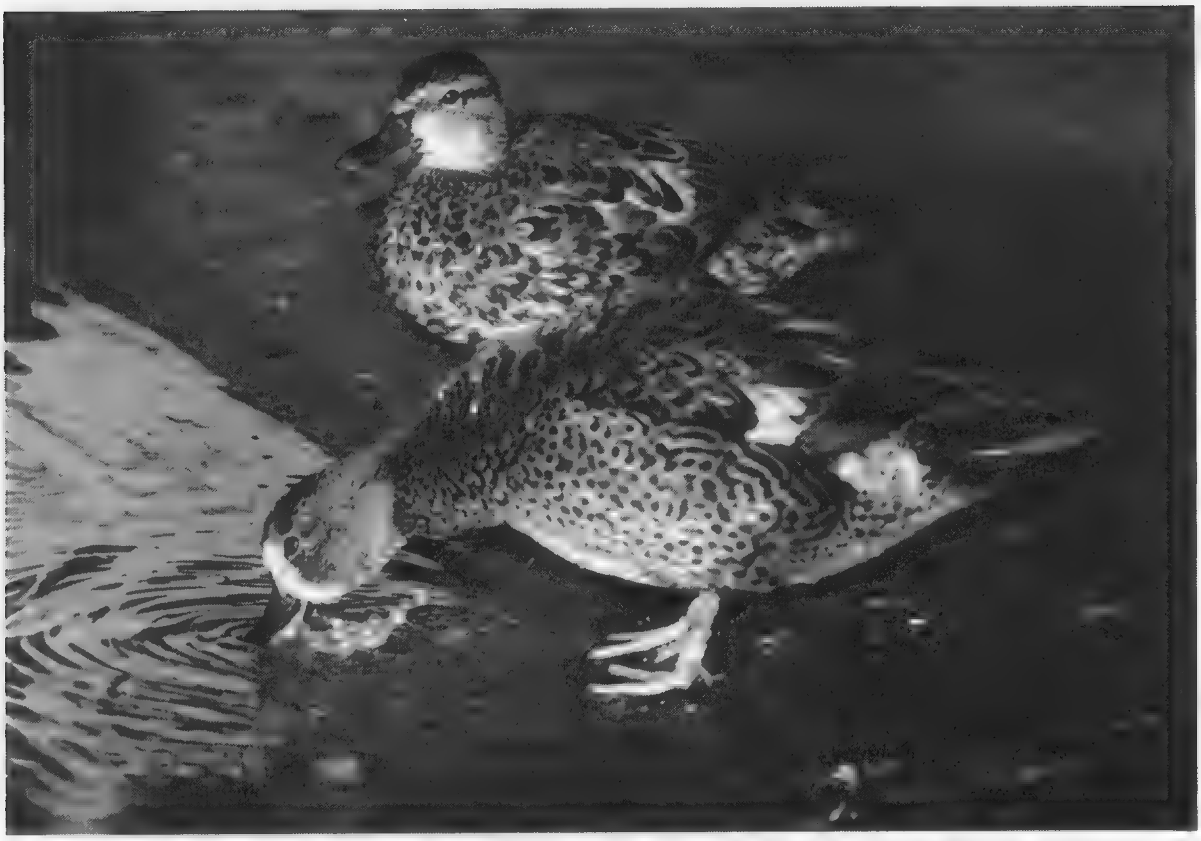
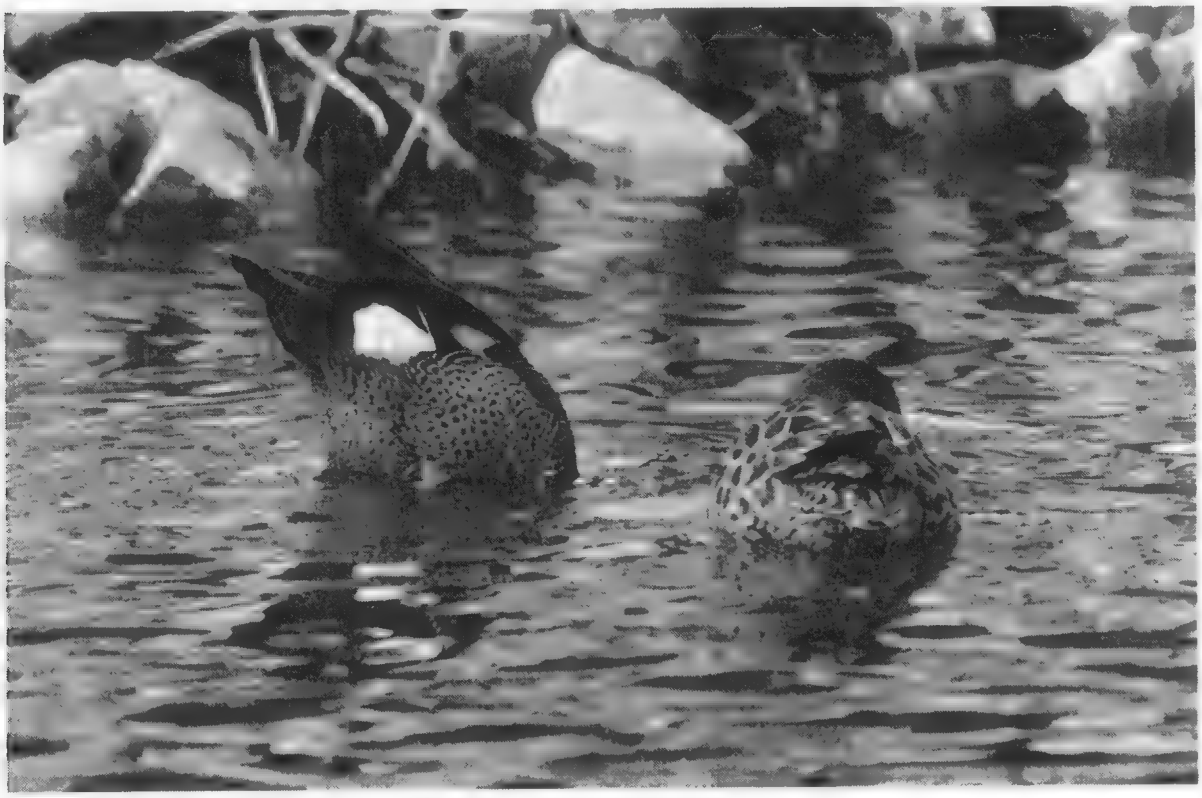


Figure 4 (*above*). A male Blue-winged Teal performing Lateral Dabbling at the edge of the water. Although males usually perform this display while swimming, they occasionally do it standing on shore. Note that the male's side is toward the female, that the feathers on his back are erect, and that part of the speculum shows. This male is not yet in full breeding plumage.

Figure 5 (*below*). A male Blue-winged Teal performing an Up-end, a display associated with pair-formation. In Up-end, the male plunges the whole fore part of his body into the water just as he does when "tipping up" to feed on the bottom. The male gives Head-dips and Up-ends, and intermediates between the two, in the same situations as Lateral Dabbling (Figures 3 and 4). His side is toward the female, the flank and back feathers raised, and the feet paddling rapidly. He may repeat these displays several times in quick succession if the female remains in a favorable position.



if in a cooperative effort to stir up food. The same performance, in a formalized manner, occurs also as a courtship display." I agree with Johnsgard (1965) that circling, head to tail, is associated with feeding and I have no evidence that it occurs as a display. Delacour and Mayr were probably referring to Lateral Dabbling, in which the male is stationary with the side of his body directed toward the female.

Head-dip and Up-end.—Head-dip consists of a brief dipping of the head and neck under the surface. In Up-end (Figure 5), the whole fore part of the body is immersed, as in the movement of "tipping-up" to feed from the bottom. Intermediates between the two displays occur.

Head-dip and Up-end are performed in similar situations as Lateral Dabbling. The male positions himself lateral to the female, erects his flank and back feathers, and paddles rapidly with the feet. The displays may be repeated several times in rapid succession, but only when the female remains long enough in a favorable position.

In my captive Northern Shovelers, the frequency of the three displays, derived from feeding movements, varied with the season. Lateral Dabbling first appeared at the beginning of the pairing season and it increased in frequency; Head-dip appeared next; Up-end came late in the period of pair-formation.

Swimming-shake.—This display differs only slightly from the normal comfort movement, being rather stiffly executed. The most distinctive feature is lateral orientation of the male's body toward the female.

Body-shake and Belly-preen.—This sequence is common in all four species. A male comes out on shore, stands broadside to the female which may be either standing or swimming close by, performs a Body-shake and then bends forward briefly into the posture of nibbling the belly (Figure 6). The form of the movement varies; sometimes he nibbles among the feathers just as in normal preening, at other times he waves his bill across above the feet without touching the body. Sometimes he repeats the movement several times in succession. When the bill touches the feathers, it is usually at a spot slightly off the center line, on the side toward the female.

Preen-dorsally and Preen-behind-wing.—I have recorded both of these displays in all four species but more rarely than Belly-preen. The birds seldom repeat these displays which are often difficult to distinguish from normal preening actions (see McKinney, 1965b).

Bathe and Wing-flap.—Northern Shovelers often perform a short series of head-dipping movements—three or four dips, not accompanied by wing-shuffling—followed by a stiffly executed Wing-flap. The Wing-flap can occur without Bathe, or the male may swim around in very tight circles a few times before rising to flap. The wings make a loud clapping noise with the final flap while, at the same time, the bird utters a few quiet "took" notes, or the wheezy versions. The male tends to perform the Wing-flap with his body lateral to the female. I have not recorded these displays in the Blue-winged Teal or Cinnamon Teal, but I did see them once in the Cape Shoveler.

Drinking.—I have seen exaggerated Drinking movements regularly only in the Northern Shoveler.

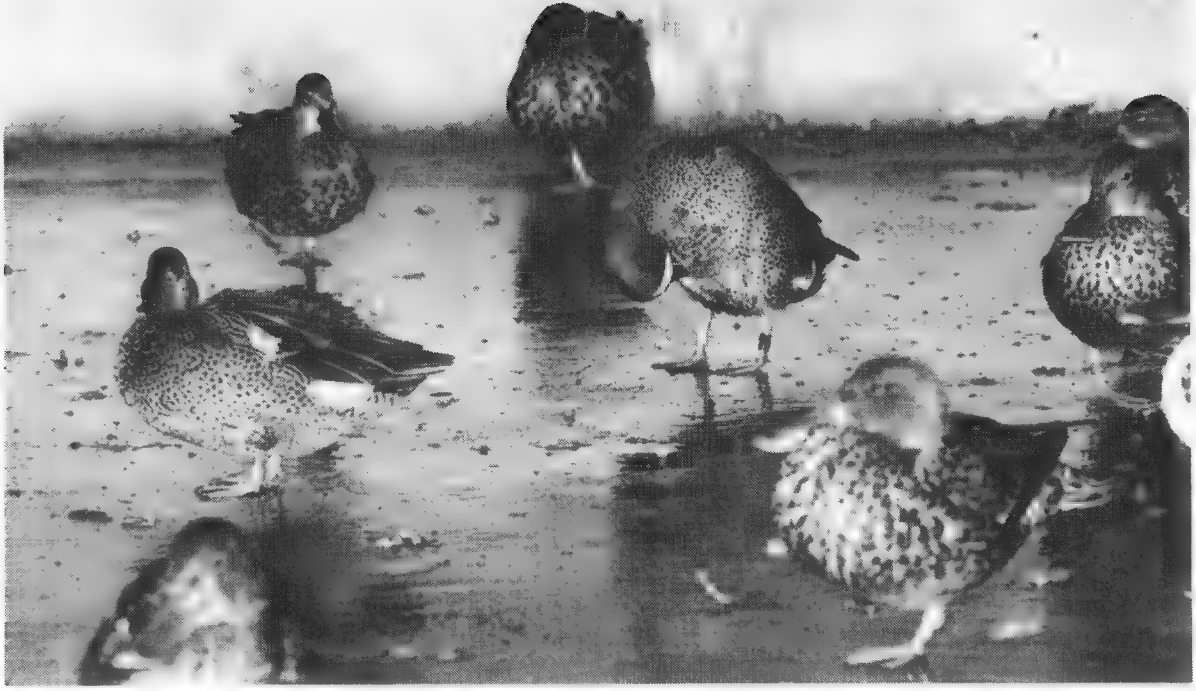


Figure 6. The male Blue-winged Teal, in the center, performing Belly-preen, a display associated with pair-formation. When a female is on shore or swimming close by, the male, standing on shore and broadside to her, gives a Body-shake and then leans over briefly and either waves the bill across the feet without touching the feathers, or nibbles the feathers as if he were preening. If he touches the feathers, they are slightly off center, on the side toward the female.

Jump-flight.—Lebret (1958, 1961) and Hori (1962) described and discussed this display. The male Northern Shoveler adopts an erect posture with the head held very high and the bill raised slightly above the horizontal. Pre-flight movements such as Head-shakes and Shakes are frequent and, just before take-off, he gives Fast Calls. When the bird rises steeply, lowering the head into a characteristic posture with the neck horizontal, the wing noise, typical of shovelers in flight, is very striking. The length of the Jump-flight is variable; most are between five and 15 yards with the male usually alighting some distance in front of the other birds in the group, and then swimming back toward them (Figure 7).

Jump-flights are very frequent in courting parties of Cape Shovelers (Siegfried, 1965). I saw this display also when males returned to their mates after aerial pursuits in the early stages of territory establishment and once after copulation. The preliminaries are just as conspicuous as in the Northern Shoveler, with marked erect posture, one or more Head-shakes, occasionally a Swimming-shake, and series of Fast Calls. At take-off and during the rapid ascent, the bird points its bill slightly upward and holds its head conspicuously erect, rather than extending it horizontally as does the Northern Shoveler. In this respect, the Cape Shoveler closely resembles the Blue-winged Teal, which adopts a similar head-up posture during the first part of the flight. (Figure 8).

On one occasion I saw a male Cinnamon Teal perform a short flight in a late spring courting party. We need more observations on wild birds to confirm the presence of a Jump-flight in this species.

Jump-flights did not appear in the captive Northern Shovelers until February and March, some weeks after other pairing displays were frequent. In Louisiana, in mid-March, wild shovelers commonly performed Jump-flights. I have seen Jump-flights in Blue-winged Teal only in the most active courting parties of wild birds after they had arrived on the breeding grounds.

These display flights seem to function in attracting the female's attention. On several occasions I noticed a direct effect on captive female Northern Shovelers when a male performed a Jump-flight. After the male alighted, one or more females ran quickly to him and performed Inciting movements beside him.

Female Displays Primarily Associated with Pair-formation

Inciting.—Lorenz (1953) described Inciting in the Garganey as consisting of alternating head-pumping and threatening movements, and he noted that the pattern was similar in the Blue-winged Teal and Cinnamon Teal. Lorenz believed that these three species form a "connecting link" between the Northern Shoveler and other dabbling ducks, the threatening component—seen in other Anatini—being absent in the shoveler. This is not the case. The female Northern Shoveler has a well-developed threatening component, and the Inciting movements are very similar in all four of the blue-winged ducks discussed here.

When birds are on land, the female may lower her head almost to the ground during threatening, and, occasionally, she makes aggressive thrusts from this posture (Figure 9). Threatening movements alternate with a marked

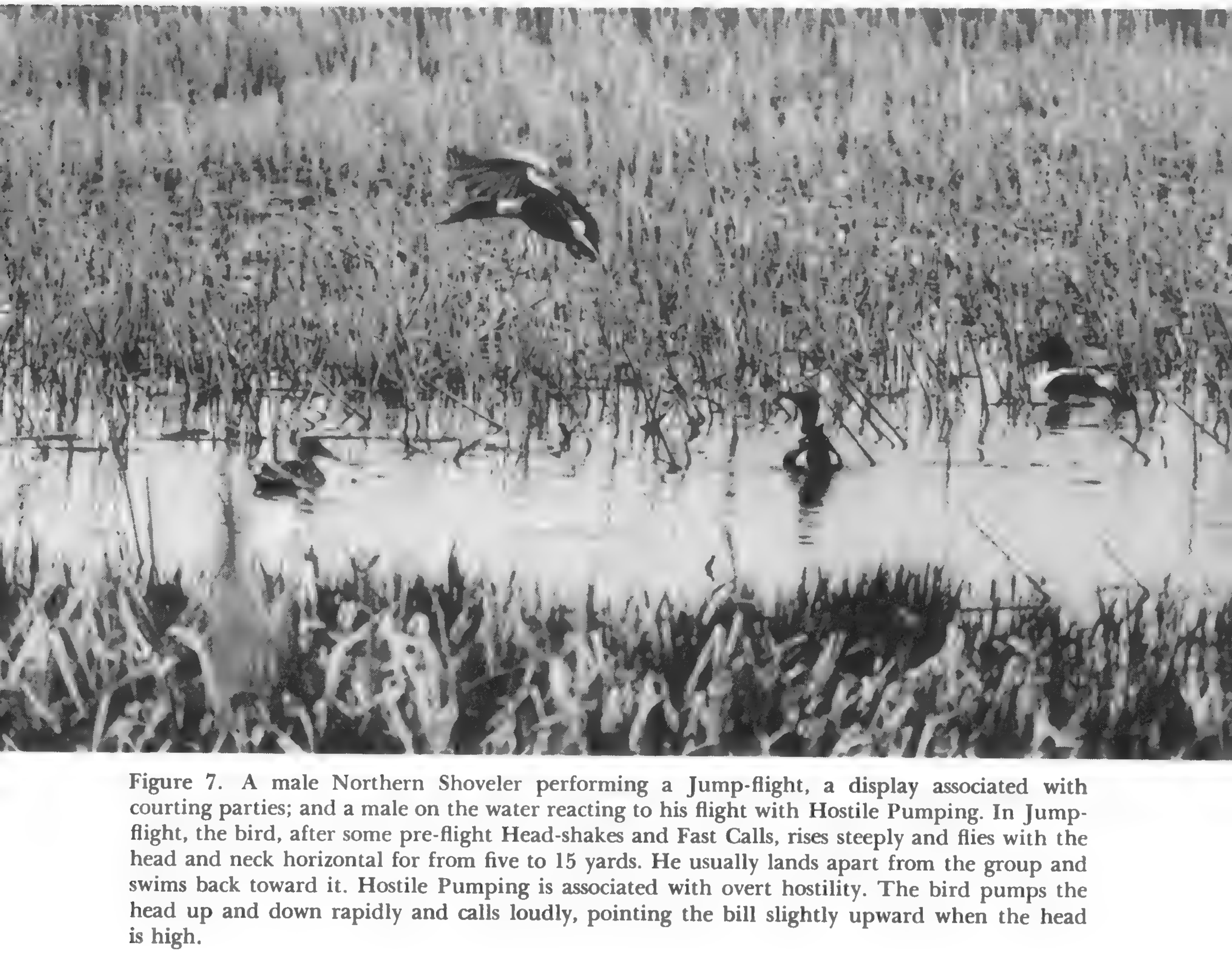
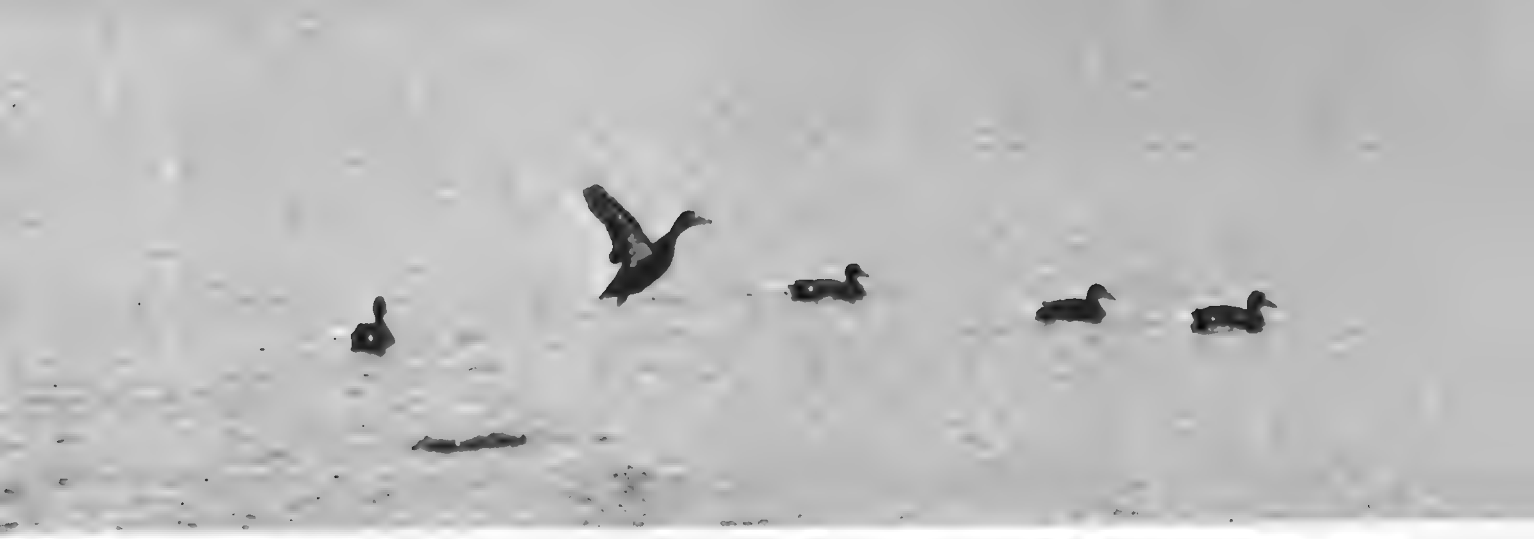
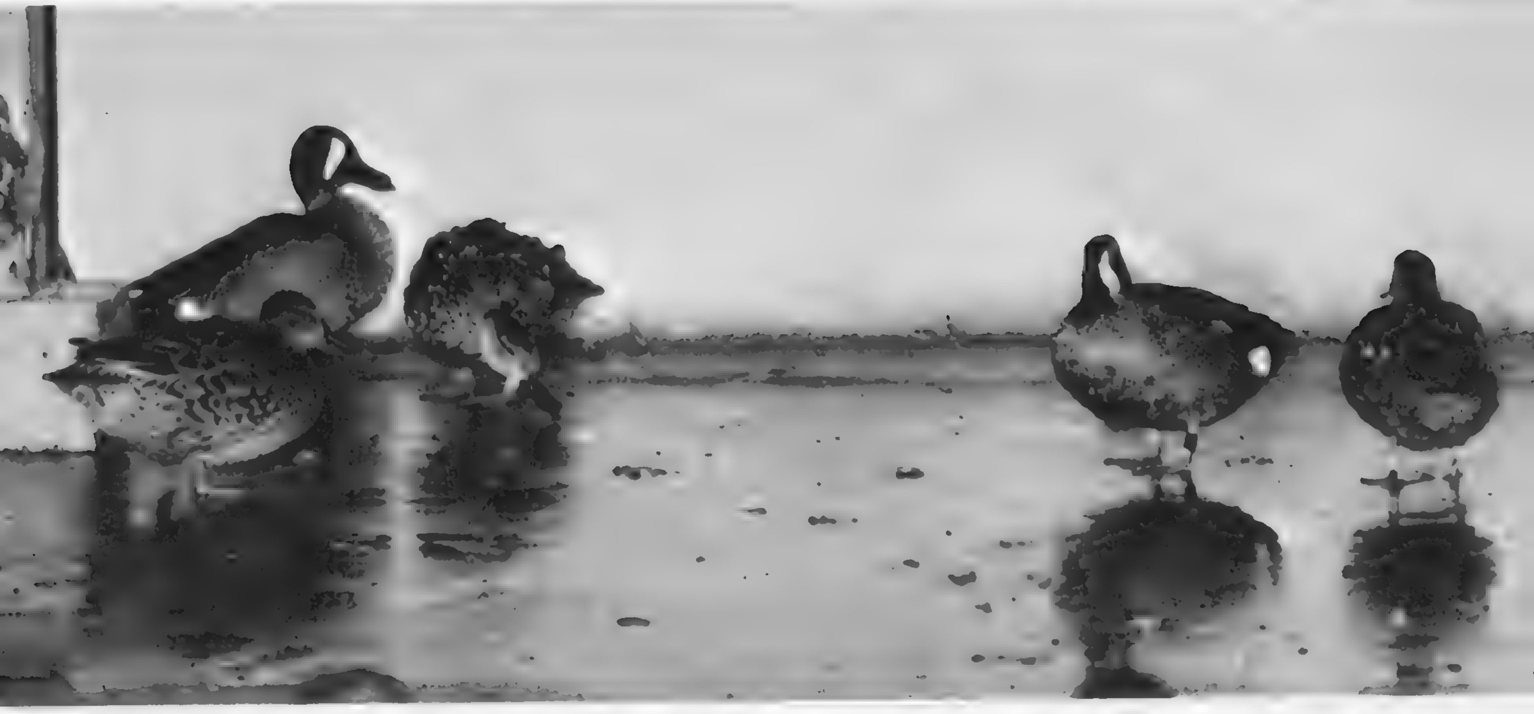


Figure 7. A male Northern Shoveler performing a Jump-flight, a display associated with courting parties; and a male on the water reacting to his flight with Hostile Pumping. In Jump-flight, the bird, after some pre-flight Head-shakes and Fast Calls, rises steeply and flies with the head and neck horizontal for from five to 15 yards. He usually lands apart from the group and swims back toward it. Hostile Pumping is associated with overt hostility. The bird pumps the head up and down rapidly and calls loudly, pointing the bill slightly upward when the head is high.





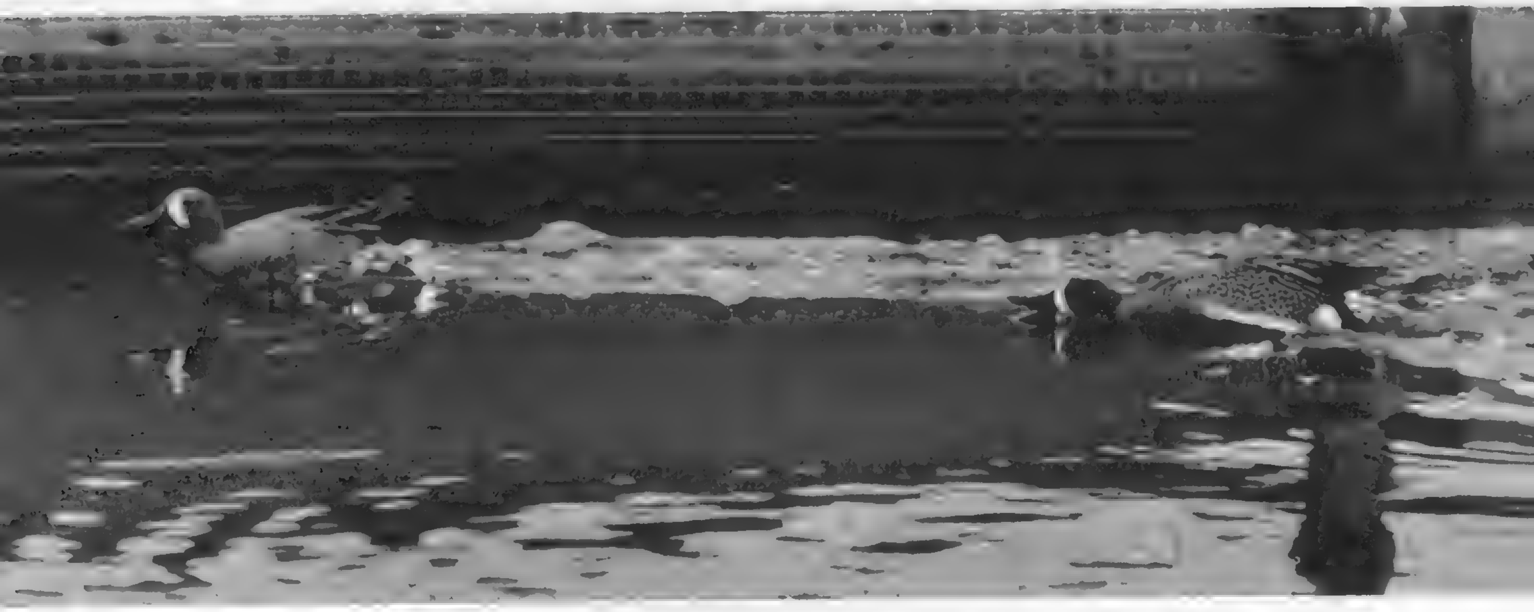


Figure 8 (*top*). A male Blue-winged Teal rising from the water at the beginning of a Jump-flight. Blue-winged Teal perform this display only in the most active courting parties. In this species the head is held erect as the bird takes off but Northern Shovelers adopt a horizontal neck posture.

Figure 9 (*middle*). The female of a Blue-winged Teal pair, on the left, directing the pointing component of Inciting at the pair on the right. She lowers her bill almost to the ground and points it at them. Sometimes in this behavior a female makes threatening thrusts as well. She may alternate this movement by stretching her head high, then lowering it again and pointing in a neck-stretch—threat—neck-stretch—threat sequence.

Figure 10 (*bottom*). A male Blue-winged Teal chasing with an energetic rush across the water. A paired male is driving away an unpaired male which has attempted to display to the female.

upward stretching of the neck, a movement corresponding to the head-up posture of the male's Hostile Pumping (see below). She directs the threatening movements straight at the other bird—for instance, a male to which the female is not paired—and performs neck-stretching toward and close beside her mate or prospective mate.

Females sometimes give several neck-stretching movements in succession, the sequence corresponding to the male's Hostile Pumping with the bill pointed upward in a similar way. During an Inciting sequence involving threat and neck-stretch and threat and neck-stretch, she gives a special call as she raises her head from the low threat posture. In all four species, the call is higher pitched and quieter than the Mallard's. It consists of a very rapid series of notes, rising in pitch and sounding like a rippling chatter. Thus, the Inciting call is many-syllabled, just as in many other Anatini, rather than one-syllabled as Lorenz (1953) suggested for both the Northern Shoveler and Garganey. There are slight differences between species. The Inciting call in the Cinnamon Teal is harsher and more rattling.

Females threatening other ducks in the vicinity of the brood also give Inciting movements even though the mate is absent. I have recorded threatening with open bill alternating with chittering calls—and sometimes head-lifting movements toward the brood—twice in Blue-winged Teal and three times in Cinnamon Teal. Further study of this behavior would be rewarding since Inciting is usually considered to be exclusively a "sexual" pattern.

TBH.—On a few occasions, I have seen female Northern Shovelers and Blue-winged Teal perform this display, though it was never as well marked as in males. They directed the display at certain males, and some of them also gave Lateral Dabbling and Belly-preen.

Lateral Dabbling.—I recorded this display in one Blue-winged Teal female which repeatedly directed it toward a certain male. Rapid paddling, feather-erection, and lateral orientation to the male were all present.

Shake and Belly-preen.—I saw these displays, similar in form to the male's, in several female Northern Shovelers and one female Blue-winged Teal.

Hostile Behavior

One can see hostile interactions at all times of year in blue-winged ducks. The level is lowest during the post-breeding period when birds are in flocks and occupied with molting and migration. Threatening and chasing become frequent during the pairing period as conflicts resulting from competition for mates are resolved. Still, at this stage, social tendencies remain strong and pairing occurs with rather little overt fighting.

During spring migration, Northern Shovelers and Blue-winged Teal travel in flocks at Delta. There is some hostility between pairs but the intensity is mild. After the pairs arrive on their breeding areas, the males become increasingly intolerant of the approach of others of their species. The attacks they direct at both males and females range in intensity from mild rushes across the surface of the water to energetic aerial pursuits (Figures 10, 11, and 12). At first the males direct most of these chases at other pairs and usually the male aims at the female. The result is the familiar "territorial defense flight" (Hochbaum, 1944), "expulsion flight" (Lebret, 1961), or "three-bird flight" (McKinney, 1965a; see Figure 13). Often the males interact in a hostile way in flight. When the females begin to incubate, the males continue to chase intruders of both sexes. Boundary disputes between males are intense and frequent.

By the time the ducklings hatch, male hostility has usually waned and the pair-bond has broken. The drakes gather together in groups and move to molting areas. The female, however, exhibits increasing aggressiveness in the vicinity of her nest as incubation proceeds, and this continues during brood-rearing, gradually waning as the young become independent. The female's hostility is a more generalized response not only to others of the same species, but also to birds or mammals which approach her nest or brood.

Hostile Pumping.—We must draw a sharp distinction between two types of "pumping" head movements in the blue-winged ducks. In Precopulatory Pumping (see below), given by members of a pair, the bill is pointed slightly downward, and only very quiet calls can be heard from the male at times. Hostile Pumping, on the other hand, is closely associated with overt hostility; the bill points slightly upward when the head is high, and loud calls accompany the head movements (Figure 14, also Figure 7). As Johnsgard (1965) noted, observers have seldom recorded this distinction.

The Northern Shoveler male gives *took* calls, fairly regularly spaced but out of phase with the head movements. In the Blue-winged Teal, the peeping calls are typically grouped in three's, the middle note being slightly higher pitched, and the head movements are faster than in the Shoveler. In the Cinnamon Teal, the head actions are faster still, and the bird gives a rapid series of typically three-syllabled, rattling *rrar* notes. The Cape Shoveler gives hoarse calls usually in groups of three or four: *chachachacha.*

At the peak of each head movement, the bill points upward at an angle of up to 30 degrees to the horizontal; at high intensities, the crown feathers are tightly depressed.

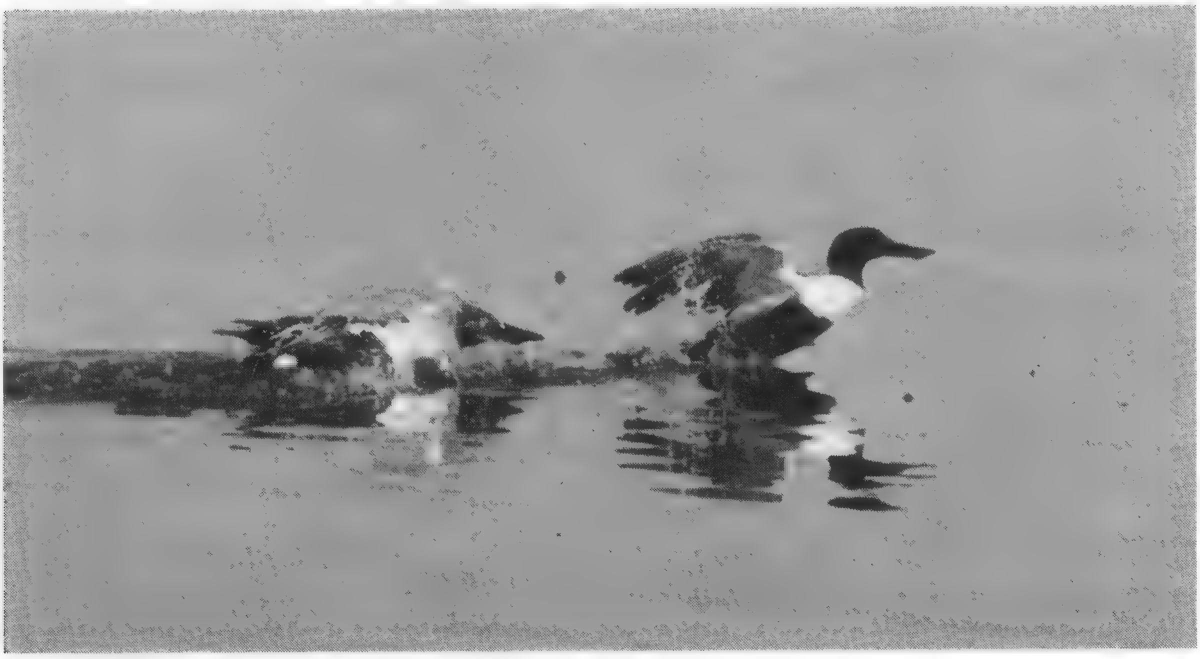


Figure 11. A male Northern Shoveler chasing an intruder in his territory. During the spring migration, the hostility between pairs is mild. After the birds arrive on the breeding grounds and have established territories, hostility increases anad boundary disputes are frequent.

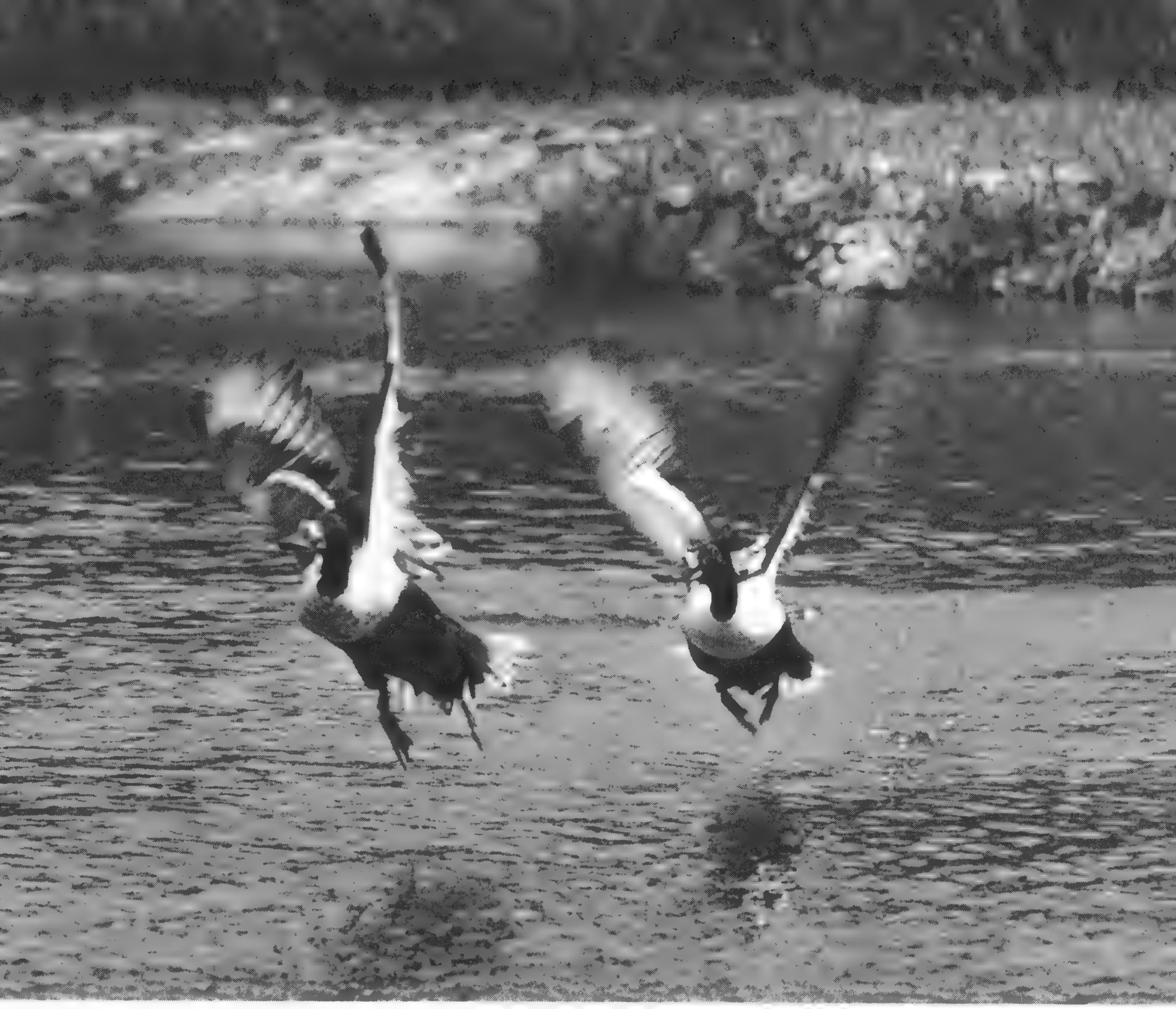


Figure 12. A male Northern Shoveler chasing another male from his territory in a Cedar Creek flight pen. As the season progresses, the chases increase from rushes across the water to flight-pursuits. The circular objects at the base of the birds' bills are plastic markers for individual identification.

Hostile Pumping, very frequent during both the pair-formation and territorial phases, is closely associated with territorial fighting and threatening, and, in less intense situations, is still obviously a response of one male to the proximity of another. Hochbaum (1944) suggested that this display serves as a threat in the Blue-winged Teal, and all evidence indicates that this is the case in all four species.

Males in courting flights often have their heads erect and they call constantly. Apparently Hostile Pumping occurs in flight just as it does in courting parties on the water.

Fighting.—Disputes between territorial males frequently take the form of energetic "fights" on the water. Similar encounters also develop occasionally between males during pair-formation. Fighting males adopt a variety of postures involving a marked sleeking of the crown feathers and an up-tilting of the bill. They lunge past each other with wings flapping on the surface of the water and bills open. Repeatedly they miss contact, merely changing positions and circling within an area of about one square yard (Figure 15). At times, both birds move in the same direction, flapping over the surface side by side. Occasionally, when the protagonists are evenly matched, they reach a

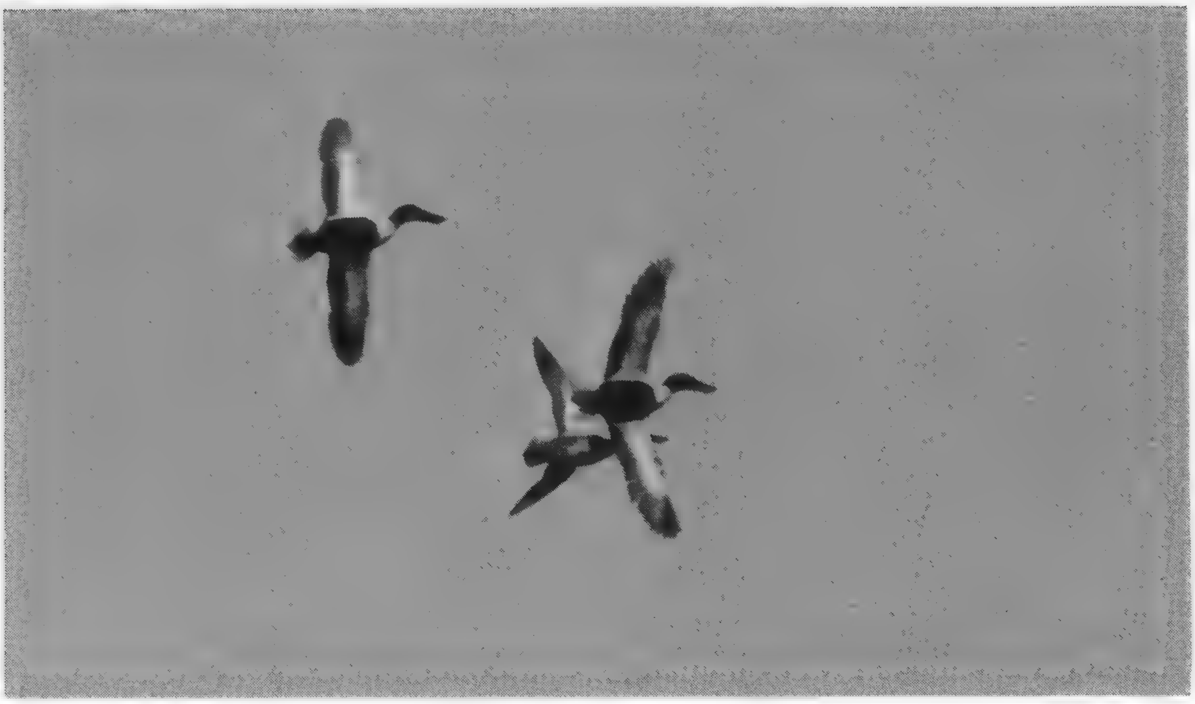


Figure 13. A male Northern Shoveler chasing a pair in a "three-bird flight." In these swift, aerial pursuits the chasing male often follows the female of the pair, but he also may engage the other male in aerial combat. Many males continue chasing intruders, both male and female, from the territory throughout the incubation period.

tense impasse. The two males sit immobile, side by side on the water, a few inches apart, with crown feathers tightly depressed. Eventually one gives way and the dispute ends with Hostile Pumping.

Superficially the fights appear to be severe, and undoubtedly the males deliver some wing-blows, but I have never seen a bird show any sign of being hurt after a fight. The encounters consist mainly of sham attacks and we might consider the impressive postures as threat displays.

While Hostile Pumping and circular fighting are especially characteristic of males, the same movements may be seen in females. Females not only give Hostile Pumping as part of the Inciting performance but also perform it independently. I have seen repeated circular fighting between two female Northern Shovelers only in the month of October, and the nature of this hostility was not clear. Fighting between a male and female occurs very rarely in Northern Shovelers.

Copulation

Copulation did not occur regularly in the captive birds until May, but in Louisiana I saw it in wild Blue-winged Teal as early as mid-March. Captive Northern Shovelers copulated as often as twice a day in the three weeks before laying and during the laying period but only rarely during incubation (McKinney, 1967). The following account is based on records of 132 apparently successful copulations in the Northern Shoveler, 12 in the Blue-winged Teal, seven in the Cape Shoveler, and two in the Cinnamon Teal.

Precopulatory Head-pumping.—These vertical head movements are similar to those of many other *Anas* species, as described by Lorenz (1953). The male's crown feathers are not depressed, as in Hostile Pumping, and his bill usually points downward at an angle of about 30 degrees to the horizontal.

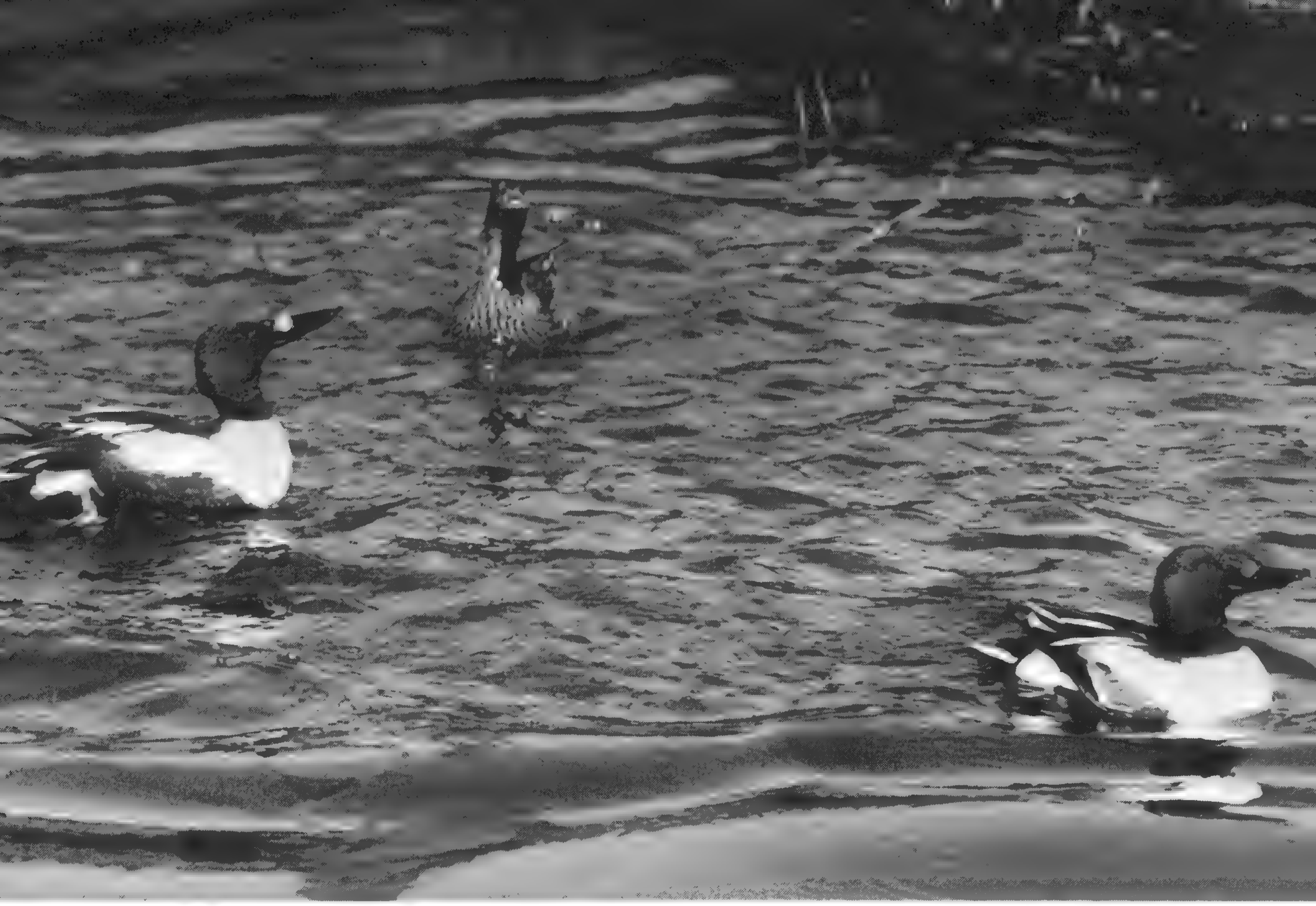
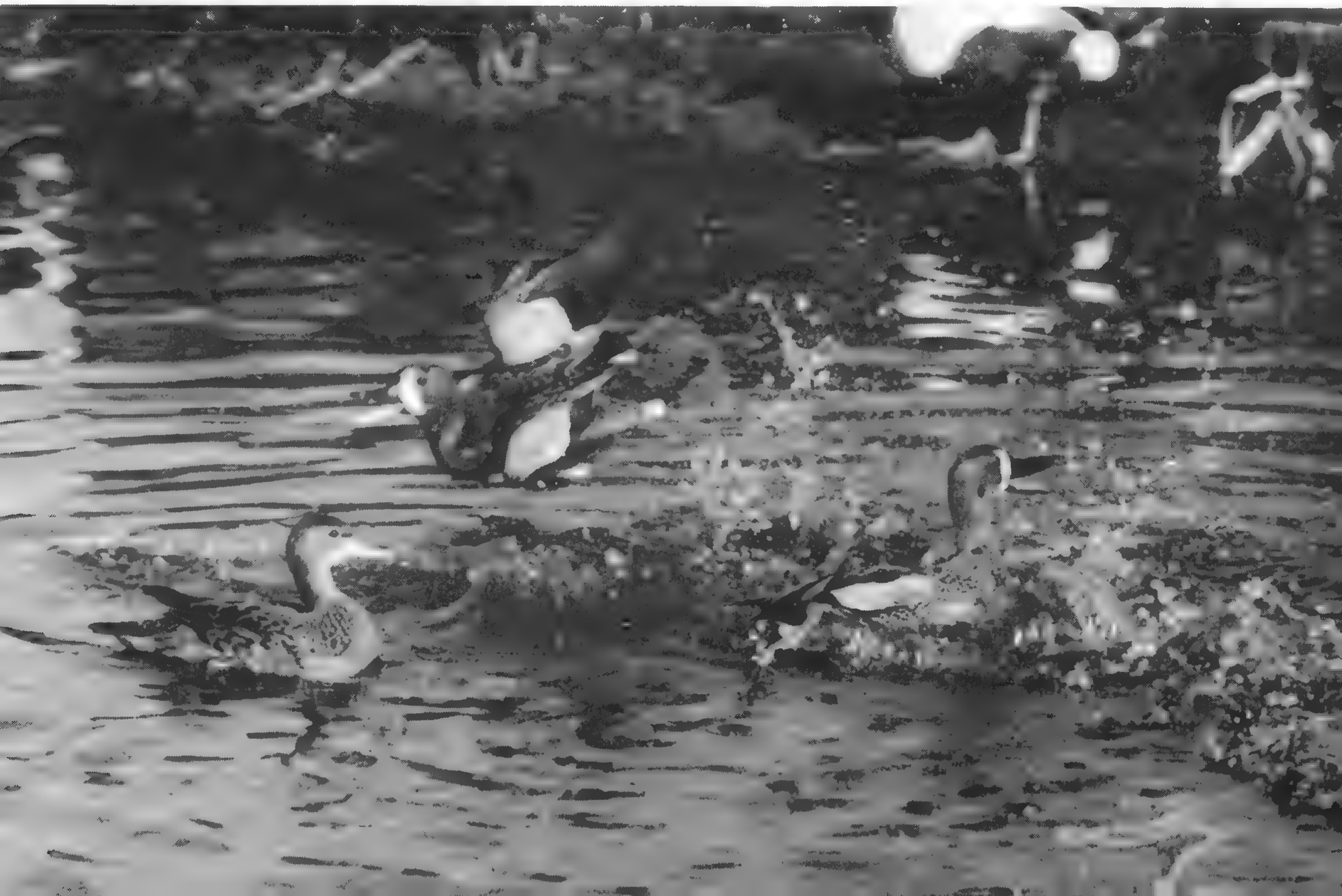


Figure 14 (*above*). A pair of Northern Shovelers at left perform Hostile Pumping during a boundary dispute. This behavior, also shown in Figure 7, apparently has threat function. Note how the bill slants up slightly. The uptilted bill, violent pumping, and loud calls distinguish Hostile Pumping from Precopulatory Pumping, a display given by members of a pair with bills slanted slightly downward and the male uttering very quiet calls.

Figure 15 (*below*). Male Blue-winged Teal "circular fighting." This occurs in territorial disputes and, occasionally, during pair-formation. With crown feathers sleeked and bills uptilted and open, the participants lunge at one another over the surface of the water. Repeatedly, they jump past each other, changing positions and circling round and round in an area of about one square yard.



Both the male and female usually perform the movements before the female adopts the prone position. Sometimes the male will repeatedly approach the female giving Precopulatory Head-pumping without eliciting a response. On other occasions, the female reacts by going directly into the copulation posture with the head stretched forward. The male sometimes continues Head-pumping after mounting and before firmly gripping the female's nape feathers in his bill. I have seen two Blue-winged Teal copulations in which the male rushed at the female, mounted rapidly, and grabbed her roughly as though raping her. In one of these instances, the male gave brief Head-pumping and, judging from their subsequent behavior, the birds were probably paired.

Calls during Copulation.—I heard males of the Northern Shoveler often, Cape Shoveler twice, and Blue-winged Teal once give rhythmical wheezy noises or very quiet calls during copulation. I suspect that these calls are usual in these species but they can be heard only under favorable conditions.

In the Northern Shoveler, I usually recorded the calls as a series of quiet, wheezy *whe* or *thic* noises. Occasionally they changed to quiet, single *took* notes, given with the same fairly fast rhythm. While I often heard these noises after the male had mounted and grasped the female's head feathers, twice they accompanied Precopulatory Pumping before the male mounted, and I heard them often as a male continued to give Pumping after mounting. Once, the volume of the calls increased to typical *tooks* as another male swam up to the copulating pair. On another occasion, the male gave a long sighing noise at the moment of copulation.

In the Cape Shoveler, I heard repeated wheezy *th* or *cuay* noises similar to those of the Northern Shoveler. The Blue-winged Teal gave very quiet *cheep-cheep, cheep-cheep* notes.

Postcopulatory Behavior. — In all four species, immediately after dismounting, the male adopts a characteristic posture with the body lateral to the female (Figures 16 and 17). He points the bill downward at an angle of about 60 degrees to the horizontal, erects the feathers of the head and neck, raises the wing-tips slightly as the tail is wagged, paddles the feet rapidly, and gives one or more calls—the Single Call or Male Decrescendo (see below). In the Northern Shoveler (Table 1), there is usually a loud, nasal *paaay,* followed by a series of double-note Repeated Calls *took-took . . . took-took* and then sometimes single Repeated Calls. Although the number of Repeated Calls varies considerably, my records suggest that a sequence of one to four double calls and one single call is the commonest pattern (Table 2). Rarely, there are single-note Repeated Calls only after the *paaay.* Occasionally, a quiet wheezy call replaces the *paaay,* or there may be only a series of Repeated Calls. The omission of the *paaay* does not seem to be related to age; it occurred in older males as well as yearlings.

The postcopulatory call of the Blue-winged Teal was a loud, high-pitched whistle *peeew,* eight times, a nasal *paaay,* four times. I heard a single *rrar* once from a Cinnamon Teal and a single loud nasal call, followed by several quieter calls, twice from Cape Shovelers.

The lateral posture and accompanying calls may be the only male postcopulatory displays. Sometimes, however, the male Northern Shoveler then performs Turn-toward-female, swinging his whole body round to face the

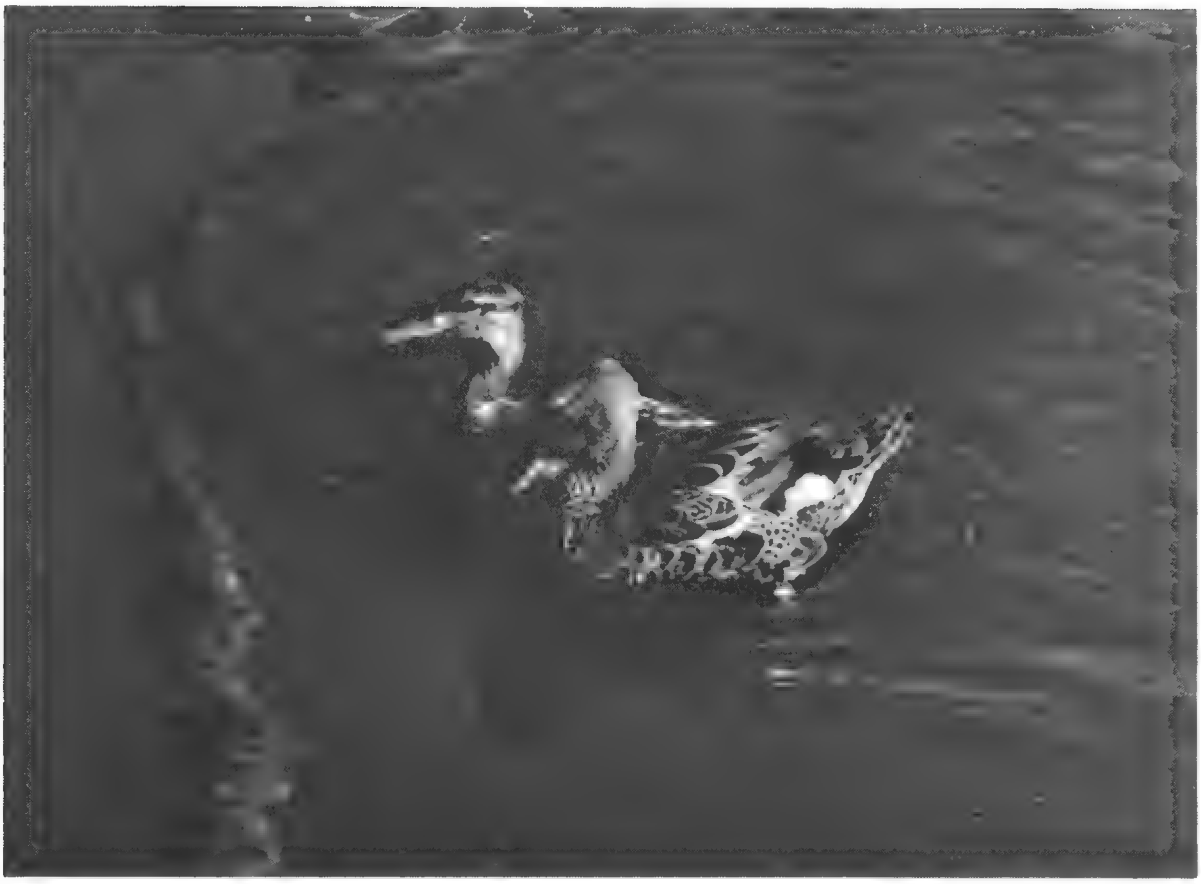


Figure 16 (*above*). A male Blue-winged Teal giving a Postcopulatory Display. Immediately after copulation the male, in the foreground, swims close beside his mate. With bill pointed down, head and neck feathers erect, and wing-tips slightly raised, he wags the tail, paddles the feet rapidly, and calls once or several times. The call of the Blue-winged Teal in this display is either a loud, high-pitched whistle *peeew* or a nasal *paay*.

Figure 17 (*below*). A male Cape Shoveler giving a Postcopulatory Display on the far side of the female. Note that his body is lateral to her and his bill points downward. In this posture he gives a single, loud nasal call, followed by several quieter calls.

female and holding this orientation for a few seconds. At other times, the male swims in a partial or complete circle around the female, maintaining his lateral body orientation. Occasionally he gives TBH or performs jerky forward and back head-nodding as Lorenz (1953) recorded. In the Blue-winged Teal, an erect posture and then two Up-end displays, performed laterally to the female, once followed the postcopulatory display. On another occasion the male gave TBH as Johnsgard (1965) recorded once. In Cape Shovelers, I saw Turn-toward-female twice and Jump-flight once after the postcopulatory display. A. Clark (quoted by Siegfried, 1965) also saw a Jump-flight in this situation and Johnsgard (1965) recorded TBH.

I have no records of female postcopulatory displays. She begins to bathe as soon as the male dismounts.

Female Displays Associated with Breeding

Loud, Repeated Quacks.—Decrescendo Calls (see below), Repulsion Calls (see below), Inciting Calls, and Quiet Broody Calls (see below) are distinctive female vocalizations readily identified by their characteristic form and by the

TABLE 1

Postcopulatory Behavior in Northern Shovelers*

Behavior	*Year*				*Total times*
	1962	*1965*	*1966*	*1967*	
Postcopulatory posture with "paaay"call	4	24	48	39	115
Postcopulatory posture without "paaay" call		6	10	1	17
Double Repeated Calls	4	16	40	37	97
Single Repeated Calls		3	12	13	28
Turn-toward-female		4	9		13
Turn-back-of-head			4	1	5
Wing-flap		1			1
Swims around female			5		5
Nod-swimming			2		2
Diving intention movements			1		1
Drink			1		1
Total copulations	4	30	58	40	132

*The records of calls are probably complete; other patterns, such as Turn-back-of-head, may have been more frequent than indicated above.

contexts in which they occur. In several other situations, females give a series of loud quacks and I am not sure that we should group them all together as variants of a single behavior pattern. For the moment, I will describe these calls as they occur in four characteristic contexts.

1. Calling at dusk during the pairing season. Captive Northern Shoveler and Blue-winged Teal females gave short series of loud, evenly spaced, single quacks from February onward. I heard these calls especially at dusk when many birds were in "flying mood." They varied much in volume and duration.

2. After flushing. When I flushed pairs of Blue-winged Teal in Louisiana in March, the females gave several—from three to seven—loud, evenly spaced quacks as they flew up and away from me. I heard similar calls when I flushed pairs of wild Blue-winged Teal and Northern Shovelers after their arrival on the breeding grounds. Females of Cape Shoveler pairs gave short series of loud quacks as they flew over me during the pre-nesting period.

TABLE 2

Number of Repeated Calls by Male Northern Shovelers after Copulation

Number of calls in series	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*Total records*
Double Repeated Calls	11	20	16	12	7	6	3	3				1	1	80
Single Repeated Calls	8	1	1		2		1							13

3. Pre-laying Persistent Quacking. On the days immediately before egg-laying, females give long series of quacks, similar in quality to those given after flushing. While the pair is swimming or standing on land, the female may call, with brief pauses between bursts, for many minutes. This Persistent Quacking occurred in many captive Northern Shovelers (McKinney, 1967), but I have heard it even more often in Blue-winged Teal. Once a female Cinnamon Teal gave similar calls while she and her mate flew around the flight pen a few days before egg-laying began. A disturbance—for instance, my appearance at a distance—often seemed to act as a stimulus; but at other times I could detect no environmental trigger. Though the notes are normally one-syllabled, one female Northern Shoveler gave double quacks when I alarmed her in the pre-laying period.

In the groups of Cape Shovelers that I observed in the pre-laying and laying phases, the females frequently gave Persistent Quacking. In the Mossel Bay birds, which had not yet begun to lay, it was especially striking at dusk when I stood up, disturbing pairs slightly and causing them to swim away from me. At Paarl, where laying was under way, females began calling spontaneously, often giving long series of quacks for many minutes with only short breaks. In a total of eight sample counts, the rate of calling was 62 notes in 37.5 seconds or 1.7 quacks per second.

4. Disturbed broody-female quacks. When flushed from the nest, especially near the time of hatching, or when disturbed with the brood, females often stay close by and utter long series of quacks until the disturbance is over. These notes vary in pitch, volume, and speed, according to the degree of the disturbance; most quacks are one-syllabled, but the Blue-winged Teal and Northern Shoveler also give double quacks.

A Blue-winged Teal, flushed from her nest as the eggs were hatching (Figures 18 and 19), gave fast, high-pitched, continuous calls: . . . *gek gek gek gekeh gek gek gek* . . .—seven calls in four seconds. Later, when I had moved out of sight, a microphone placed near the nest recorded quieter, deeper toned, and slower calling but still with a few double notes, and just before she returned to the nest: . . . *puk* . . . *puk* . . . *puk* . . . *puk* . . .—four calls in five seconds.

A captive Northern Shoveler, which had lost her brood a few days previously, gave single *gek* calls, while I remained out of sight, and changed to double *quaquak* calls when I showed myself.

Noisy quacking has been noted from a female Cape Shoveler disturbed with her brood (Siegfried, 1965).

Repulsion.—As a result of the small home range, the aggressiveness of the paired male, and the long duration of the pair-bond, an incubating female normally joins her mate when she leaves the nest and thus is protected from the rape attempts of strange males. Occasionally, however, if the female does not find her mate or if he is not sufficiently aggressive, she is chased and gives Repulsion calls and postures like those of the Mallard (Lorenz, 1953). The notes have a similar form in the Northern Shoveler, Blue-winged Teal, and Cinnamon Teal — a single, loud, querulous *quack* followed by a series of quieter, rapid *gaek* notes. One captive Northern Shoveler gave high-pitched, squeal-like calls while being chased. Female blue-winged ducks seldom assume the bent-neck posture, so characteristic of Repulsion in the Mallard, more than momentarily.

Distraction Display.—Incubating birds sit closely and are often difficult to flush from the nest. Late in incubation, females of all four species perform a Distraction Display ("Feigning Injury"), flapping over the ground or water with simultaneous wing actions (Figures 18 and 19). Bent (1923), Hochbaum (1944), Sowls (1955), and Brand (1961) described this behavior.

Broody Threat Posture.—Some tame, captive-raised birds refused to leave the nest even when touched. One wild Blue-winged Teal, possibly an escaped captive, alternately pecked at my hand and adopted a posture with fanned tail and feathers erected on the back, flanks, and rump, exposing the oil gland to view (Figure 20). Tame, broody Mallards react similarly (McKinney, 1969).

Quiet Broody Calls.—I placed a microphone by the nests of a Blue-winged Teal and a Northern Shoveler at the time of hatching. Both females made rapid and extremely quiet notes when they returned to the nest, with occasional "trills" apparently composed of the same notes repeated very rapidly: *pip pip pip pip ppppppp* in the Blue-winged Teal and *bub bub bub bub bubububub* in the Northern Shoveler. After the females had settled on their nests, they continued to call from time to time with very quiet notes similar to those given by females leading broods.

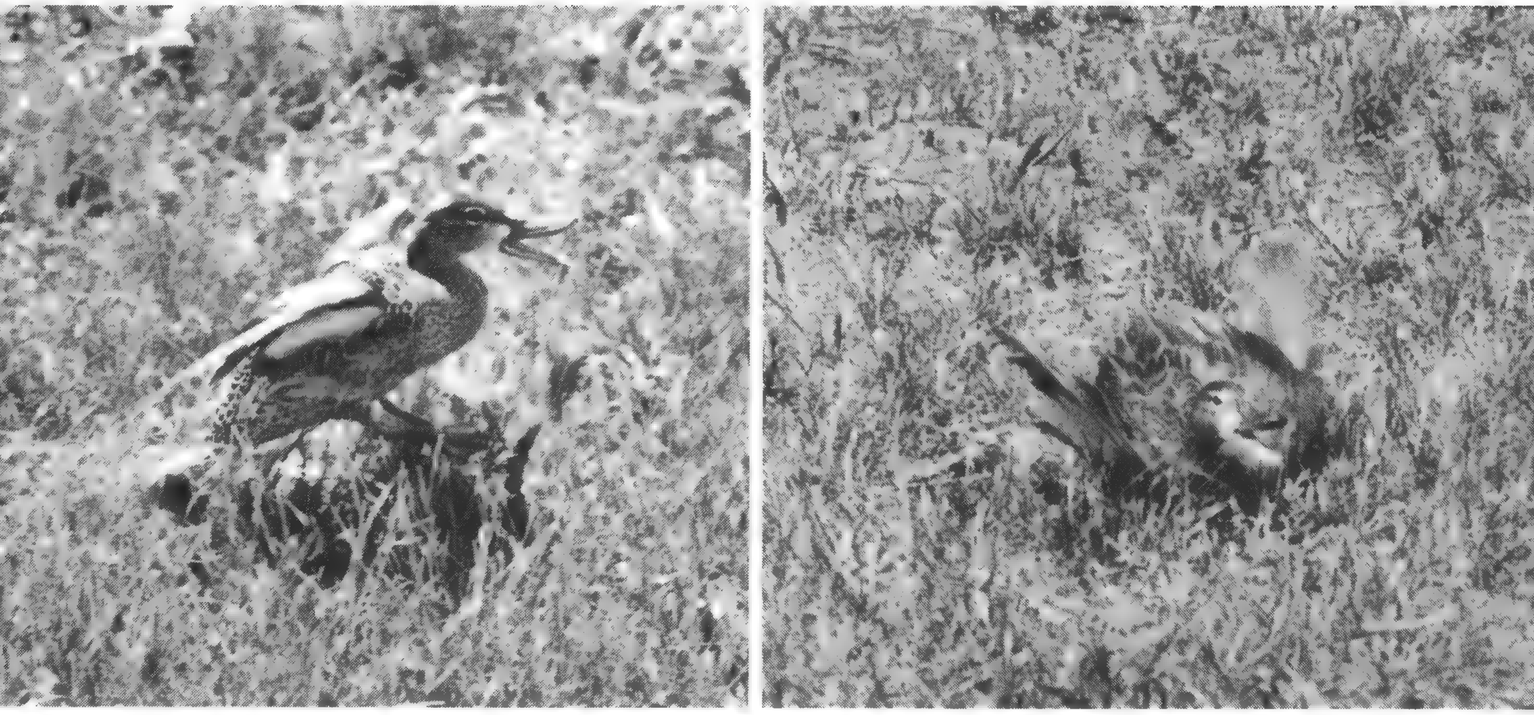


Figure 18. Female Blue-winged Teal performing Distraction Displays. When flushed from the nest, particularly as the eggs are about to hatch, females often stay close by and utter a long series of quacks that vary in pitch and volume with the intensity of the disturbance. Most quacks, under such conditions, are one-syllabled although the Blue-winged Teal and the Northern Shoveler also give double quacks.

Calls Characteristic of the Non-reproductive Season

Male Single Call and Male Decrescendo.—In the three North American species, these calls are frequent during fall and early winter but are heard rarely after pair-formation begins. During the breeding season, the only time one hears them is after copulation. The males give the calls from a posture very like that from which a female gives the Decrescendo—the head is raised, but not fully erect. I have heard these calls mostly from birds standing on land.

The Single Call of the Blue-winged Teal is a loud, high-pitched, piercing whistle *peew* or, in some individuals, a low-pitched, nasal *paay*. The Male Decrescendo consists of the *peew* whistle followed by a short series of quieter, low-pitched, evenly spaced *pew* calls: *peew . . . . pew . . pew . . pew . . pew.*

The Single Call of the Northern Shoveler is a nasal *paaay*. The Male Decrescendo has the same rhythm as in the Blue-winged Teal: *paaay . . . . took-took . . . took-took.*

The Single Call of the Cinnamon Teal is a quiet *rrar,* and I once heard a single loud explosive call from a Cape Shoveler. I have not heard a Male Decrescendo in either of these species.

The Male Decrescendo of the Blue-winged Teal and Northern Shoveler consists of a Single Call plus Repeated Calls and has the same seasonal distribution as the Single Call. The birds give both vocalizations from the same posture and without any obvious environmental stimulus. I could never predict which would occur and probably we should consider both calls as variants of a single behavior pattern.

Female Decrescendo.—Lorenz (1953) described the Northern Shoveler's Decrescendo as a "single cry, rising and dying down." While this description might be appropriate for some individual shovelers, it is not accurate for the species as a whole. I have known a Blue-winged Teal which gave one-syllabled Decrescendos, but in all four blue-winged ducks there are usually several or many syllables. There is great individual variation in the number of syllables and also in the pattern of the complete call. Most Northern Shovelers give one, two, three, or four long notes, each with a downward inflection: if there are several long notes, they are progressively lower pitched. Immediately after these long notes there is usually a series of three to nine shorter ones, each with approximately the same pitch. In the two teal species, there is often only one long note followed by a variable number of short notes—one to 14 recorded.

The notes of the Northern Shoveler's Decrescendo are deeper, longer, and uttered more slowly than those of the two teal. The Cinnamon Teal's Decrescendo has a hoarse, rattling quality.

Each individual tends to give a call of a certain pattern. The number of syllables varies somewhat, but the general form is so constant that I have learned to recognize many birds by their Decrescendos.

Females give these calls throughout the year (Figure 21), except during the incubation and brood-rearing periods, and they are frequent in juveniles from an age of about two months. There is a marked diurnal rhythm of calling with peaks occurring during the morning and evening twilight periods.

Pre-flight Signals

Waterfowl perform a variety of movements before taking wing and, especially in swans and geese, also give loud calls. Comfort movements such as body-shake, wing-flap, and stretches are frequent, while various intention

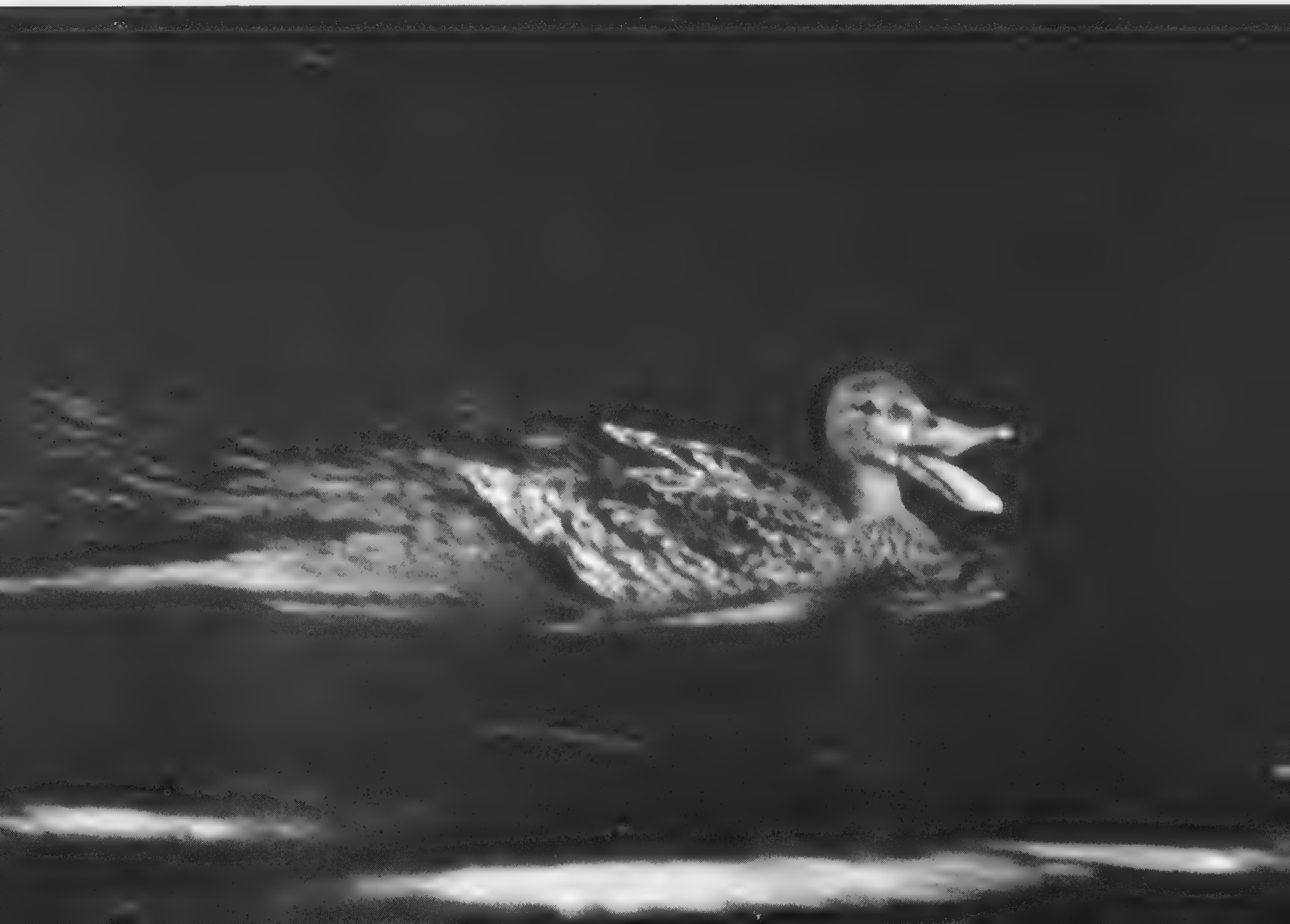


Figure 19. A female Northern Shoveler giving a Distraction Display while with her brood. Disturbed by the photographer, she flaps over the water, giving loud calls.

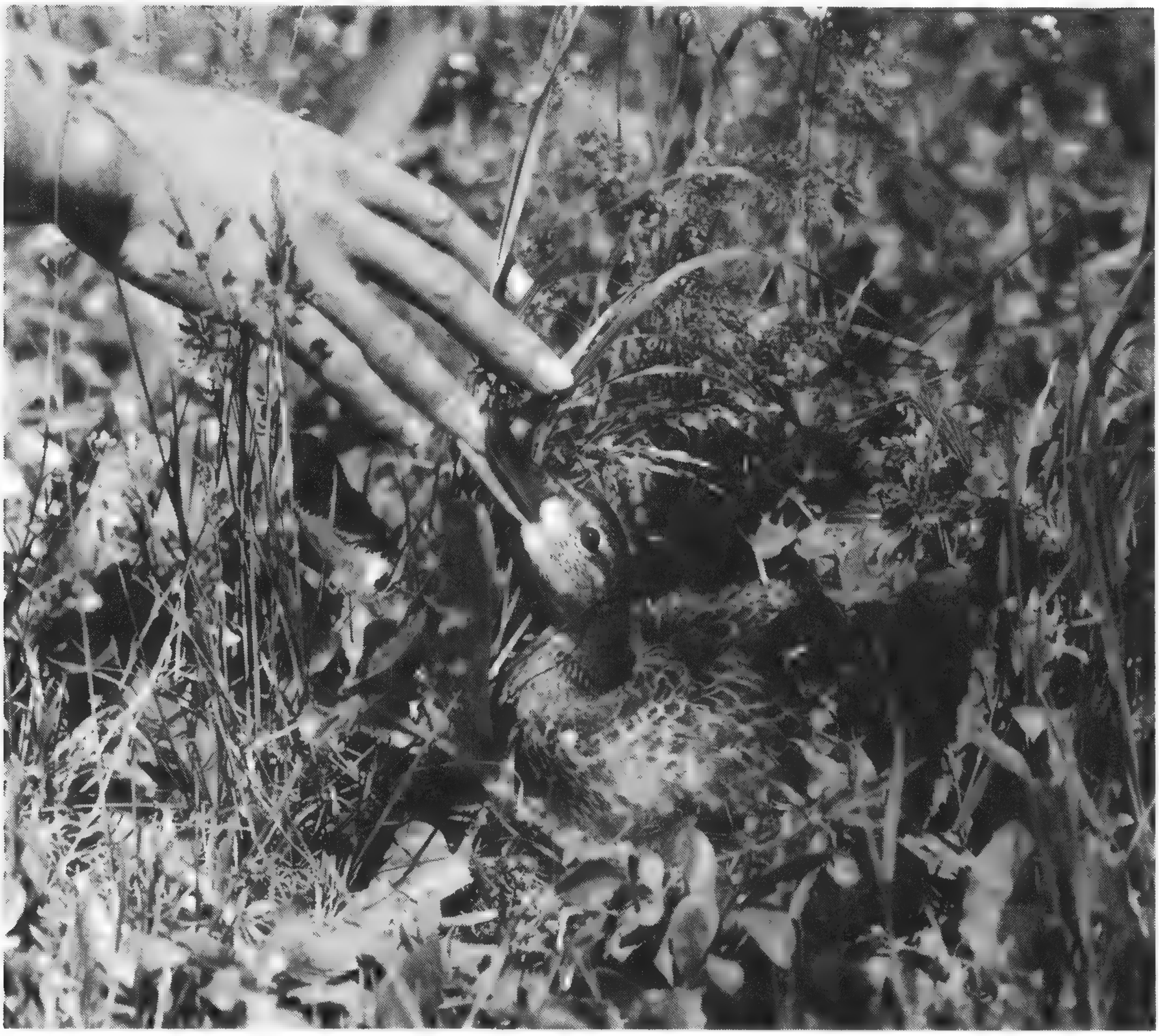


Figure 20. A female Blue-winged Teal adopting a Broody Threat Posture. Some females are so broody that they refuse to leave the nest even when touched. This bird, possibly an escaped captive, alternately pecked at the hand and posed with the tail fanned and feathers erected on the back, flanks, and rump.

movements involving the head or forepart of the body are common (McKinney, 1965b). Which of these movements function as signals indicating the intention to fly is uncertain. In the blue-winged ducks, as in other Anatini, the adoption of an erect posture, facing into the wind, lateral Head-shaking, and vertical Head-thrusting are probably most important.

Conclusions

Differences in the Displays of the Four Species

Almost all display movements occur, with similar form, in all four species (Table 3). The exceptions are Bathe plus Wing-flap which I noted only in the two shoveler species and Drinking which occurred regularly only in the Northern Shoveler. There are differences in posture at the start of the Jump-flight, the head being held erect in Cape Shoveler and Blue-winged Teal and more horizontal in the Northern Shoveler. The Jump-flight is very frequent in the two shoveler species; it occurs, but probably less often, in the teal. In addition, of course, there are differences in speed correlated with body size, such movements as Hostile Pumping being much more rapid in the teal than in the shovelers.

Most vocalizations occur with similar pattern in the four species, but male Fast Calls have been noted only in the two shovelers and the distribution of the Male Decrescendo and Single Call is uncertain.

There are striking differences in the quality of male calls, each species making one or two basic types of sound. Repeated Calls, for instance, sound very different in each species, the units being a deep *took* in the Northern Shoveler, a whistling *pew* or nasal *pay* in the Blue-winged Teal, a quiet rattling *rrar* in the Cinnamon Teal, and a hoarse *cawick* in the Cape Shoveler. These differences are equally striking during Hostile Pumping. The nasal *paaay* call of the Northern Shoveler, however, as heard in the Single Call, Male Decrescendo, and postcopulatory display, is quite similar to the corresponding call of the Blue-winged Teal.

The quality of female calls is similar between species. All females make quack-like sounds arranged in a variety of patterns. There are slight species differences in quality, shoveler quacks being longer and deeper pitched than corresponding teal calls and, as with movements, speed is faster in the smaller species.

Male breeding plumages differ greatly in colors and patterns between the four species, so that male appearance, from every angle, is distinctive.

In summary, most display movements and calls are present in all four species, but the shovelers have a few patterns which are absent or infrequent in the two teal species. Almost all display movements are similar in form in the four species, but the plumage patterns, demonstrated in the male displays, are strikingly different. The quality of most male calls differs conspicuously between species.

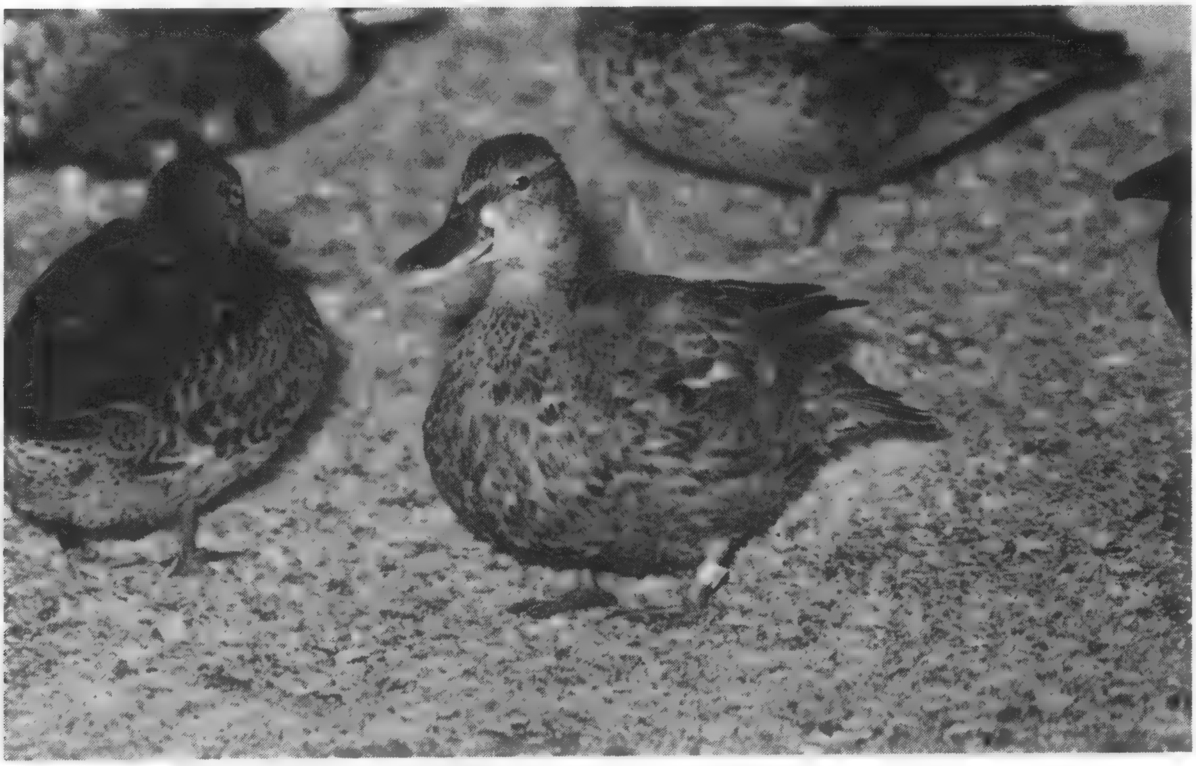


Figure 21. A female Blue-winged Teal giving a Decrescendo Call. Decrescendos, heard most often during the morning and evening twilight, vary greatly in number of syllables and pattern. In the Blue-winged Teal there is usually one long note followed by a series of short notes. Each female tends to have a distinctive Decrescendo and this call appears to be important in individual recognition.

TABLE 3

The Occurrence of Homologous Displays in the
Four Species of Blue-winged Ducks

	A. clypeata	*A. smithi*	*A. discors*	*A. cyanoptera*
Pair-formation displays				
Repeated Calls	X	X	X	X
Fast Calls	X	X		
TBH	X	X	X	X
Lateral Dabbling	X	X	X	X
Head-dip	X	X	X	X
Up-end	X	X	X	X
Swimming-shake	X	X	X	X
Preen-dorsally	X	X	X	X
Preen-behind-wing	R	R	R	R
Body-shake + Belly-preen	X	X	X	X
Bathe + Wing-flap	X	X		
Jump-flight	X	X	R	(1)
Drinking	X		(1)	
Inciting	X	X	X	X
Hostile behavior				
Hostile Pumping	X	X	X	X
Circular Fighting	X	X	X	X
Copulatory behavior				
Precopulatory Head-pumping	X	X	X	X
Calls during copulation	X	(2)	(1)	
Postcopulatory Display	X	X	X	(1)
Female breeding displays				
Persistent Quacking	X	X	X	X
Broody-female Quacks	X	X*	X	X
Repulsion	X	X*	X	X
Distraction Display	X	X*	X	X
Non-reproductive calls				
Male Single Call	X	(1)	X	
Male Decrescendo	X		X	
Female Decrescendo	X	X	X	X

* Reported by Siegfried (1965).
R Rare

Characteristics of the Display Repertoires

The major distinctive feature of pair-formation displays in these four species is the use of three signal movements derived from feeding behavior—Lateral Dabbling, Head-dip, and Up-end. As Johnsgard (1965) suggested, these displays occur in similar situations and probably serve similar functions as the Grunt-whistle, Head-up-tail-up, and Down-up displays of other *Anas* species. Although other species of Anatini are known to perform the Jump-flight — for example, Mallard and Green-winged Teal — it is an especially important display in the shovelers, judging from its high frequency and ritualized form. Similarly, while Belly-preen occurs in some other species (McKinney, 1965b), it appears to be the main display given by males on land in all four blue-winged ducks. In the Green-winged Teal, Bridling occurs as well as Belly-preen in such situations (McKinney, 1965c). The ritualized Wing-flap is a notably conspicuous display in the Northern Shoveler and Lorenz (1953) reports that it is very frequent in the Garganey. Its significance in the other blue-winged ducks is uncertain.

Repeated Calls and Turn-back-of-head are frequent displays in courting parties. While TBH occurs in many species of ducks and Johnsgard (1960) emphasized the important role that it appears to play in pair-formation, the Repeated Calls have had little attention. Series of Burps in the Green-winged Teal (McKinney, 1965c) and Slow Raehbs in the Mallard (Weidmann, 1956) occur during social courtship in situations similar to those in which the blue-winged ducks give the Repeated Calls. All these species give the same vocalizations in response to disturbance or mildly alarming stimuli. In pairing situations, Repeated Calls seem to have the function of attracting the female's attention, thus playing a role similar to the "song" of many birds. We need to search for homologous vocalizations in other dabbling ducks to determine whether the repetitive pattern is a widespread characteristic.

Behavior associated with hostility is characterized by specialized threatening and fighting methods. Hostile Pumping seems to be diagnostic of the blue-winged ducks. Although fighting in other species of Anatini probably involves some circling, this pattern is especially frequent and apparently ritualized in the blue-winged ducks. The form of the female's Inciting movements, including pronounced head-lifting as in Hostile Pumping, is also distinctive.

Copulatory behavior is similar to that of other Anatini except for the characteristic form of the male's postcopulatory display which may prove to be peculiar to the blue-winged ducks.

Of the calls occurring outside the breeding season, the male's Single Call is of special interest. It probably corresponds to some of the displays labeled "Burp" in other dabbling ducks but homologies will have to be worked out with caution. In the Garganey, for instance, Lorenz (1953) described the Burp as common during social courtship and noted its close similarity to the Burps of species such as the Pintail (*Anas acuta*), which are also given during pairing. In the Northern Shoveler and Blue-winged Teal, however, the Single Call and Male Decrescendo are not characteristic of the pairing season; the only time they are heard during the reproductive period is in the postcopulatory display.

Discussion

The spectacular diversity in display movements, calls, and plumage patterns within the Anatini presents many challenging problems. In the case of species occupying the same area, much attention has been drawn to the need for specifically distinct signals in preventing hybridization (Sibley, 1957; Johnsgard, 1963; Mayr, 1963). But selection against hybrids is a secondary process operating only after stocks have diverged in isolation and subsequently come into contact. Many specific differences in social behavior and plumage features are likely to have arisen as populations diverged from their parent stocks under the influence of varied environmental conditions. Thus we may expect the communication system of each species to have developed distinctive features as it evolved in association with a multitude of interwoven structural, physiological, ecological, and ethological adaptations. The need to consider such factors in attempting to unravel the selection pressures which have shaped the displays of each species has become obvious from recent comparative studies of behavioral adaptations in other birds (e.g., Cullen, 1957; Tinbergen, 1963, 1967; Crook, 1964).

The first stage in an investigation of this sort—preliminary description of displays and comparisons between species—leads to some tentative generalizations. The second stage involves attempts to correlate specific differences in displays with differences in other aspects of the biology of the species concerned. This procedure may lead to hypotheses which can be investigated further by comparative or experimental studies. In this discussion I will concentrate on the possible effects of feeding behavior and the territorial system on the communication system of the blue-winged ducks. In a few cases, factors which may have influenced specific differences within the group are considered.

Feeding Behavior.—Dabbling ducks have several feeding methods but the relative importance of each varies from species to species (Szijj, 1965). Shovelers feed mostly at the water surface by dabbling and in shallow water by dipping the head and neck under the surface. In slightly deeper water they tip up. Szijj (1965) found that tipping-up is a more important method in the Mallard and Pintail than in the Northern Shoveler. Blue-winged Teal fairly commonly dive for food at Delta, and Northern Shovelers occasionally dive also, but in general this feeding technique is relatively unimportant in blue-winged ducks. In the four species discussed here very little food is gathered on land.

During the adaptive radiation of the Anatini the ancestral blue-winged duck stock likely became specialized for feeding while swimming, with particular emphasis on surface dabbling and head-dipping. Other groups exploited different feeding methods, the Mallards and Pintails using tipping-up to a greater extent, the wigeons developing an ability to graze, and a few species, such as the Cape Teal (*Anas capensis*), becoming efficient divers. I suggest that feeding by surface dabbling facilitated the evolution of Lateral Dabbling as a pairing signal in the blue-winged ducks. In the early stages of ritualization it would have been possible for a bird to continue ingesting food while signaling, and this may still be the case in present-day forms. This behavior could have been a significant factor for a species dependent on plankton-straining, long periods of surface dabbling being required for ingestion of small food items in great numbers. Siegfried (1965) suggests that the Cape Shoveler is "obliged to devote a proportionately greater amount of time to feeding activities than many other dabbling ducks" and I suspect that the same is true for the Northern Shoveler. Goodman and Fisher (1962) use the same argument to account for the relatively small body size of the Northern Shoveler. We need a detailed comparative study of feeding behavior in Anatini to check this idea.

This argument raises the interesting possibility that specialization for feeding on surface plankton, as seen in present-day shovelers, was the primitive condition in the group and that existing small-billed forms, such as the Blue-winged Teal, have evolved from shoveler-like ancestors. This is the reverse of the sequence suggested by Delacour and Mayr (1945).

The addition of calls, feather erection, and the lateral body orientation component would have been relatively simple developments increasing the conspicuousness of Lateral Dabbling. The black color of the male's bill, a characteristic of blue-winged ducks, may function as a further reinforcing structure. The bill would normally be seen by other birds against a light background of sky-reflecting water surface. Also the bright yellow eyes of most males in the group — red in the Blue-winged Teal and Cinnamon Teal — are conspicuous during this display which is performed close to the female with the head held stationary.

While surface dabbling had obvious advantages as the basis for a pairing display, it is perhaps surprising to find that the head-dipping and tipping-up feeding movements have also been used since the male cannot continue to observe the female while his head is submerged. Apparently this disadvantage has been overcome by so shortening the time involved that Head-dip and Up-end displays are momentary events. Perhaps the close association between the three movements, during feeding, facilitated their ritualization as a group, just as several comfort movements, linked with bathing, have become ritualized as precopulatory signals in the Common Eider, *Somateria mollissima* (McKinney, 1961).

In all three displays, derived from feeding, the speculum is exposed by a slight wing movement, and probably the spotted sides, white flank patches, and brightly colored scapular feathers also show to advantage during these displays. During Up-end, in particular, the orange legs are conspicuous against a background of black tail coverts. The white flank patch, as seen in the Blue-winged Teal and Northern Shoveler, appears to have been secondarily lost in the Cape Shoveler. A "ghost" of this plumage pattern can be seen in male Cape Shovelers and presumably it was present in ancestral forms.

Displays derived from feeding movements may prove to have a wider distribution within the Anatini than we currently recognize. While noting the great development of these displays in the blue-winged ducks, Johnsgard (1965) records them also in the African Black Duck (*Anas sparsa*)—apparently Lateral Dabbling and Head-dip at least. He suggests that "none of the Mallard-like ducks possess such a display." I have a few records of Up-end after hostile encounters in the Mallard, and R. I. Smith (1968) recorded feeding movements during pair-formation in the Pintail, but we need more observations on context and body orientations.

The situation may be similar to that emerging on the distribution of displays derived from preening in ducks (McKinney, 1965b). While the highly ritualized Preen-behind-wing is a frequent display in such species as the Mallard and Green-winged Teal, it occurs only rarely in the Blue-winged Teal and Northern Shoveler. From casual observations on Argentine Red Shovelers at Slimbridge, I am convinced that the display is very frequent in this species. Johnsgard (1965) also recorded it. Apparently a group of species can have a large repertoire of homologous displays, each with significant specific variations in their frequencies. Comparable quantitative information on the relative frequency of homologous displays in different species is time-consuming to compile, yet obviously this must be one of the next steps if we are to proceed further with this type of investigation.

The Territorial System.—Before nesting begins, pairs of these four species of blue-winged ducks become antisocial, each pair confining its activities to a small home range within which the male responds aggressively to intruders of the same species. In the two shovelers especially, there is very little overlap between adjacent territories and energetic fighting between neighboring males is frequent.

Associated with this highly developed territorial behavior, pair-bonds are strong and long lasting, aerial pursuits are usually short, and assaults on strange females, ending in rape attempts, are rare. In these respects, the blue-winged duck system differs from that of such species as the Mallard and Pintail where home ranges are large with much overlap, pair-bonds are weaker and break earlier, aerial pursuits are often prolonged and wide-ranging, and rape attempts are frequent (Dzubin, 1955; McKinney, 1965a; R. I. Smith, 1968).

I suggest that Hostile Pumping evolved in association with this system of small discrete territories, in response to the need for a threat display effective at a distance. I have often seen a territory-holding male Northern Shoveler or Blue-winged Teal react to the appearance of an intruder by Hostile Pumping when the other bird was many yards distant. At times this display appears to make the intruder retreat. As I have described, Hostile Pumping is also very frequent during disputes at close quarters. In these situations it probably serves a corresponding threat function to the "Rabrab" calling with raised bill in the Mallard and the Bill-up of the Green-winged Teal (McKinney, 1965c) and I suspect that all these displays had a common origin. The Mallard and Green-winged Teal, however, give these displays only at close range and they do not seem to have a specialized distant threat display. We need further comparative studies to test this suggestion.

If Hostile Pumping evolved from the same ancestral behavior pattern as the Mallard and Green-winged Teal displays involving up-tilting of the bill, it is noteworthy that only in the blue-winged ducks do the females have the corresponding pattern. Again, I suggest that this is involved with the territorial system. Although head-pumping movements are often performed by females as part of Inciting during pair-formation, such movements occur also during territorial encounters between pairs and, in such situations, they could serve to support the male's threat displays, the members of a pair working as a team to discourage intruders.

We expect a ritualization of fighting methods in strongly territorial species where boundary disputes are frequent. The blue-winged ducks have specialized in circling, and neighboring males appear to resolve many disputes with little bodily contact. Energetic and spectacular as these fights often are, I have never known them to result in injuries.

Wing Noise.—On a still day, the sound of a Cape Shoveler or Northern Shoveler taking wing can be heard for a great distance. The characteristic rattling sound distinguishes these birds from other dabbling ducks. During the territorial season, I suspect that the noise of a male rising from his territory is readily identified by neighboring males, and it seems likely that the wing sounds play a role in advertising the bird's presence and location. Wing noise is also striking during two displays used in pair-formation, the Jump-flight and the Wing-flap. Whether the structural changes required to produce the sound evolved in association with territorial advertisement or as a reinforcement for these displays is difficult to say. The other duck most famous for its wing noise, the Common Goldeneye (*Bucephala clangula*), has a ritualized short flight (McKinney, 1965b), but several other species not noted for wing noise also have display flights. We need more comparative information; it would be premature to generalize at this stage.

In addition to the wing noise, a shoveler's Jump-flight is made more conspicuous by preparatory movements and calls and the optical effect is reinforced by morphological features. The assumption of an erect posture, the orientation into the wind, the Head-shakes and calls increasing in volume, all draw attention to a bird about to perform a Jump-flight. The loud wing rattle comes at the moment of take-off. The bright orange legs dangle against a background of black under tail coverts as the flight continues to the accompaniment of quieter calls. As the bird alights in front of the female, he exposes the black back and blue, white, and green wing patches. It seems more likely that the blue wing coverts evolved as a reinforcing structure for the Jump-flight than that they were linked with the evolution of wing-preening displays as suggested by Lorenz (1953) and Johnsgard (1965). Preen-behind-wing is rare in the Northern Shoveler and Cape Shoveler, species in which the Jump-flight is highly ritualized. Furthermore, this Preen-behind-wing display does not fully expose the upper wing coverts to view.

Jump-flights occur in the Blue-winged Teal but they are probably less frequent than in the shovelers. I have heard no distinctive wing noise.

The conspicuousness of Bathe plus Wing-flap as a pair-formation display sequence in the Northern Shoveler appears to be enhanced by the loud rattling sound produced by the wings. I recorded this sequence once in the Cape Shoveler and it could be an important signal in this species too. It appears to be absent in the two teal species.

Male Plumage Patterns and Calls.—I have pointed out that certain color patterns of the male plumages and soft parts are especially conspicuous during various displays with the implication that these morphological features have evolved to reinforce the optical effect of these displays. In many cases, calls accompany display movements and apparently serve to draw attention to the bird giving the display. The evidence strongly supports the general conclusion that the breeding plumages, calls, and display movements of males have acquired their characteristic form in response to selection pressures favoring efficient signaling in social situations associated especially with pair-formation, copulation, hostile encounters, maintaining contact between the members of a pair, and integrating flock activities. The signaling requirements in each of these situations are somewhat different, and the communication system of each species must represent a compromise resulting from many different selective forces.

In a few cases, it is becoming a little easier to understand why the communication system of each species of duck has special characteristics. Feeding methods, habitat, and vulnerability to predators appear to have influenced the degree of sociability and readiness to fly in Steller's Eider (*Polysticta stelleri*) with associated effects on certain characteristics of the displays (McKinney, 1965d). Feeding methods and territorial behavior seem to have been important in determining the type of displays evolved by the group of blue-winged ducks. There are several hints that differences between the displays of the two shovelers and the two teal, discussed here, have been influenced by these factors also. There remains the problem of why the pattern of male breeding plumages and the quality of male calls should be so different between the four species.

It is likely that distinctive male breeding plumages and male calls are important in preventing hybridization with sympatric species, but this remains to be demonstrated. We need experiments on the features used in sex-recognition and species-recognition, especially in the light of the work by Schutz (1965) on sexual imprinting in ducks and the revealing study by N. G. Smith (1966) on isolating mechanisms in gulls. We must investigate further the possibility, most recently discussed by Weller (1968), that the reduced plumage dimorphism of many ducks in the southern hemisphere may be associated with a tendency for permanent pairing and a need to begin breeding at short notice in areas with irregular rainfall. Experimental evidence on the factors influencing the female's choice in competitive pairing situations is badly needed. Students of duck behavior now have an exciting opportunity to contribute to this field of behavior evolution. The time is ripe for major advances in our understanding of the neglected question: Why does *this* species behave in *this* way?

Summary

Displays of the Northern Shoveler (*Anas clypeata*), Cape Shoveler (*A. smithi*), Blue-winged Teal (*A. discors*), and Cinnamon Teal (*A. cyanoptera*) are described briefly and compared.

Striking male displays associated with pair-formation in all four species are Repeated Calls, Turn-back-of-head, Belly-preen, Jump-flight, and three displays derived from feeding behavior—Lateral Dabbling, Head-dip, and Up-end. A ritualized Bathe plus Wing-flap sequence occurs in the Northern Shoveler. Female Inciting includes a pronounced upward neck-stretching component. Several male displays — Turn-back-of-head, Lateral Dabbling, Belly-preen — are given rarely by females.

Hostile Pumping is a conspicuous and frequent display associated with aggressive encounters both during pairing and territorial phases. Males engage in circular fights, repeatedly lunging past one another with flapping wings.

Precopulatory Head-pumping is similar to that of other Anatini. Quiet rhythmical calls occur during copulation. Males have a characteristic post-copulatory posture with calls.

Females give loud repeated quacks in several situations: at dusk during the pairing season, after flushing, during the days before laying, and when disturbed with a brood. Repulsion, Distraction Display, Broody Threat Posture, and Quiet Broody Calls are similar to the corresponding patterns in the Mallard.

During fall and early winter, males of the North American species have a distinctive Single Call, and a related Male Decrescendo is frequent in the Northern Shoveler and Blue-winged Teal. These appear to be the same calls as occur in the postcopulatory situation. The pattern of female Decrescendo calls varies greatly in individuals. This call is not heard during the incubation and brood-rearing periods.

Most display movements and calls are present in all four species, but the shovelers have a few patterns which are absent or infrequent in the two teal species. Display movements are similar in form but male plumage patterns are very different in the four species. The quality of most male calls also differs conspicuously between species.

The three displays derived from feeding, the highly ritualized Jump-flight in the shovelers, the Belly-preen, and Repeated Calls, are considered to be especially important patterns during pair-formation in this group. Hostile Pumping and the ritualized fighting methods are noteworthy components of aggressive encounters.

The possible influences of feeding behavior and the territorial system on the evolution of the displays are discussed. If ancestral blue-winged ducks were specialized for surface filter-feeding, the ritualization of dabbling might have been facilitated, enabling the birds to signal while continuing to feed. Hostile Pumping and ritualized fighting methods appear to be well suited to the needs of maintaining small discrete territories. Wing noise in the shovelers may be involved in territorial advertisement, but it is also conspicuous during the Jump-flight and Wing-flap displays.

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THE SHOULDER-SPOT DISPLAY OF GROUSE

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Grouse of the family Tetraonidae use a variety of postures and displays to express different intensities of alarm. For example, acoustic signals, derived from wing-beats and sometimes calls, communicate alarm necessitating precipitous flight. This startling, noisy flush of a frightened grouse is acoustically quite different from the sound made by a territorial male performing a "flutter-jump" display or a song-flight. Thus, on a lek of Sharp-tailed Grouse (*Pedioecetes phasianellus*) males may take off in flutter-jumps many hundred times without ever precipitating any alarm behavior in their companions, but the noise from a frightened bird may send them all away in flight.

From a blind in a lek, I have deliberately frightened a single bird in such a way that his companions on the opposite side of the blind could not see the stimulus. Yet his alarm-flush usually caused the others to leave with him and, in many cases, to fly over the blind, thus coming toward and passing directly over the cause of his fear.

Since most species of grouse are gregarious for at least part of the year, we are not surprised to find that they use a variety of signals in communicating fear and other moods to their flock companions. Among most species the responses to potential danger are upright or prostrate postures with sleeked plumage; other responses to certain kinds of disturbance may be flight intention movements, such as bobbing, neck-craning, or raising the crown feathers, all signaling an intention to fly away.

I wish to discuss here a display that in some species expresses fear while in others seems to have evolved new meanings.

Discussion

A white shoulder spot is one of the most conspicuous markings on a male Black Grouse (*Lyrurus tetrix*) or a male Capercaillie (*Tetrao urogallus*) when displaying. The females of these two species also display a white shoulder spot on occasion as do many other species of grouse.

How is this white spot produced and controlled by the bird? In all species of grouse the lesser wing coverts on the underside of the proximal, or shoulder end, of the patagium (the skin extending from wrist to shoulder) are white or at least partially so. Normally, when the bird is at rest, these feathers lie out of

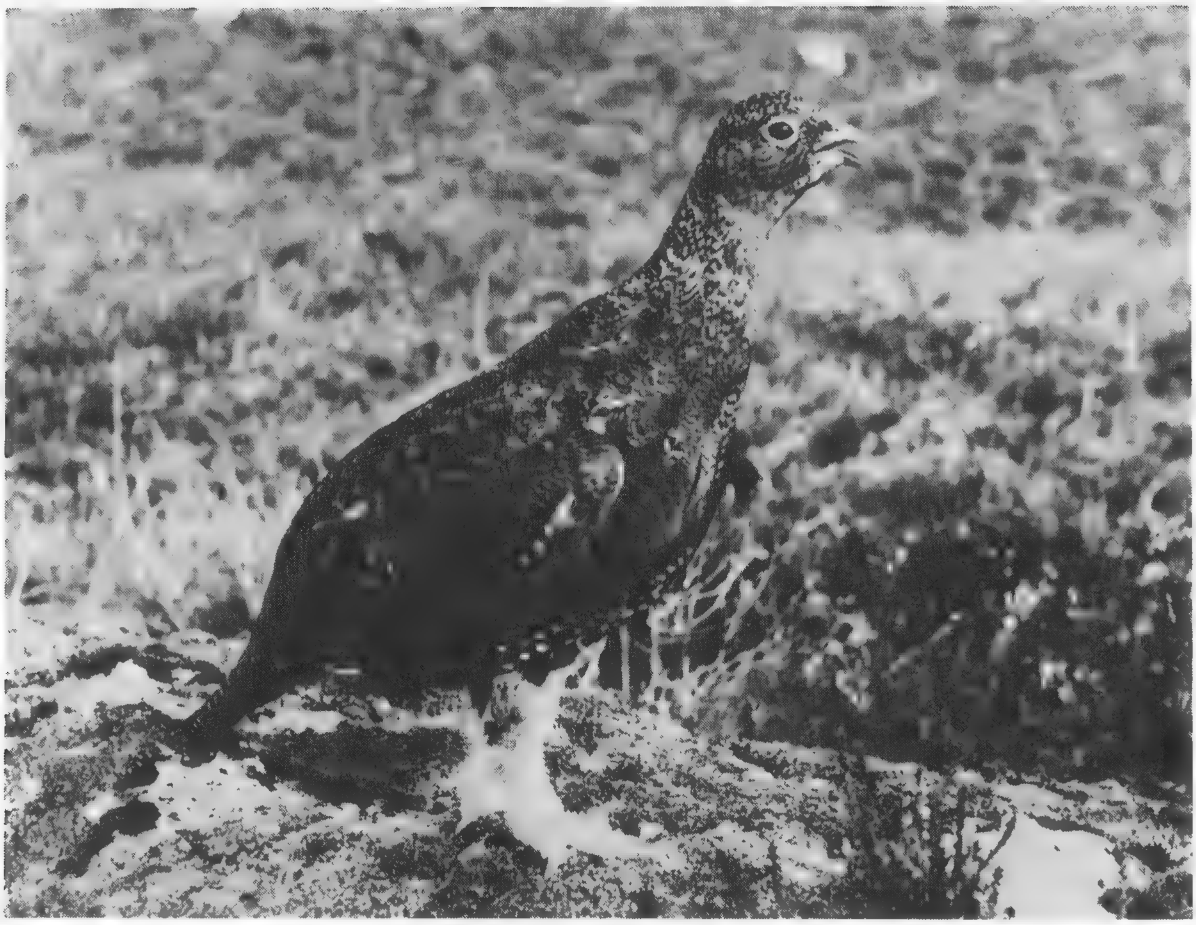

Figure 1. An unusually tame male Red Grouse displaying a small white shoulder spot. His sleeked upright posture and folded combs indicate an element of fear in his mood. Photograph by N. Picozzi.

sight under the patagium. The shoulder area and carpal, or wrist, joint in turn are covered by the anterior scapulars and feathers on the side of the body. Grouse apparently have the ability to alter the position of these white feathers so that they lie in view on the dorsal, or upper surface, of the patagium adjacent to the shoulder. The spot becomes visible when the wrist joint is extended from the contour feathers which normally cover it at rest.

Figure 1 shows the Scottish Red Grouse (*Lagopus s. scoticus*) in a "standing alert" posture (Watson and Jenkins, 1964). Note that the combs over the eyes are folded down and almost covered by the lateral crown feathers. The tail is down, the neck is sleek—not swollen as in aggression—and the wings are outside the anterior side feathers. A small white shoulder spot is visible.

I have seen captive Red Grouse fly to the far end of their pen and stand bobbing with flight intention movements while holding their wings as in Figure 1 and showing a more prominent white shoulder spot than in the illustration. The posture of this Red Grouse suggests the origin of the shoulder-spot display. The everted patagium feathers are most commonly visible under the stimulus of an alarm so mild that it does not prompt instantaneous flight. In such circumstances, communication of intention to fly away is possible and often desirable in this gregarious species.

Since the Scottish Red Grouse is the only race of *Lagopus* that retains a dark, heavily pigmented plumage throughout the winter, only in this race is the white shoulder spot visible throughout the year. I have not seen and can find no record of a shoulder-spot display in any species of *Lagopus* that turns white in winter – the Rock Ptarmigan (*Lagopus mutus*), the White-tailed Ptarmigan (*L. leucurus*), or the races of Willow Ptarmigan (*L. lagopus*). Although such a display could function only during those months when these birds carry their dark plumages, further study may reveal that all forms of the genus *Lagopus* perform this display.

The shoulder-spot display, as commonly performed by most species, clearly does not function as a flight intention signal. Ritualized and, in some cases, specially emphasized by the enlargement of the feathers concerned, it has been so emancipated from its original function, that the meaning of the signal may differ with different species and communicate a variety of moods.

For example, Hamerstrom and Hamerstrom (1960) observed that the shoulder-spot display of the Greater Prairie Chicken (*Tympanuchus cupido*) is performed only at times of high excitement. Just before copulation both sexes may show the spot. Note in Figure 2 that both the male, about to mount, and the female, having assumed a soliciting posture, display the spot. Contour feathers cover shoulder areas of the other two males, concealing any white feathers. The Hamerstroms point out that the birds may show the spot also just before or during battle, sometimes while "booming," and sometimes just before death.

I have seen Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) produce a shoulder spot prior to copulation and during fighting.

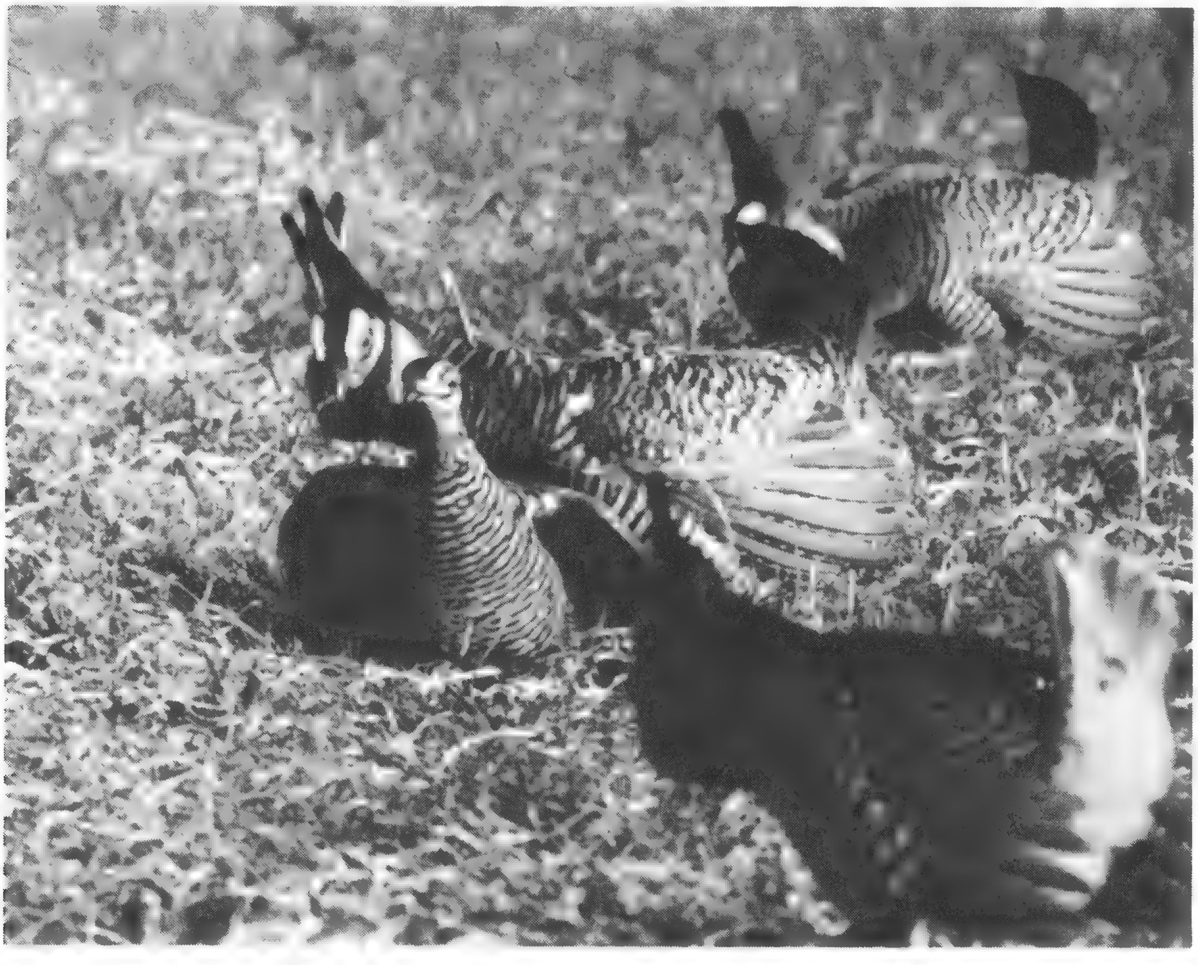

Figure 2. Both the male Greater Prairie Chicken, about to mount, and the female in the precopulatory posture are showing white shoulder spots. Note that neither of the other males is displaying the spot. Photograph by the author.

In some populations of the Sharp-tailed Grouse, both sexes display the white shoulder spot during periods of sexual excitement such as just before copulation or while fighting (Lumsden, 1965). Figure 3 illustrates a prominent white spot displayed by a male Sharp-tail in Montana. This banded bird was skirmishing with a neighboring male and giving a tail-rattling display when the picture was taken. A captive male also showed a spot while I was removing him from a holding crate.

Male Sage Grouse (*Centrocercus urophasianus*) display a shoulder spot when fighting, but not during courtship. Figure 4 shows two males standing head to tail with shoulders opposite in the fighting alignment characteristic of this species. The male on the left reveals a shoulder spot. Subdominant yearling males show a spot when being chased by older dominant males. I have

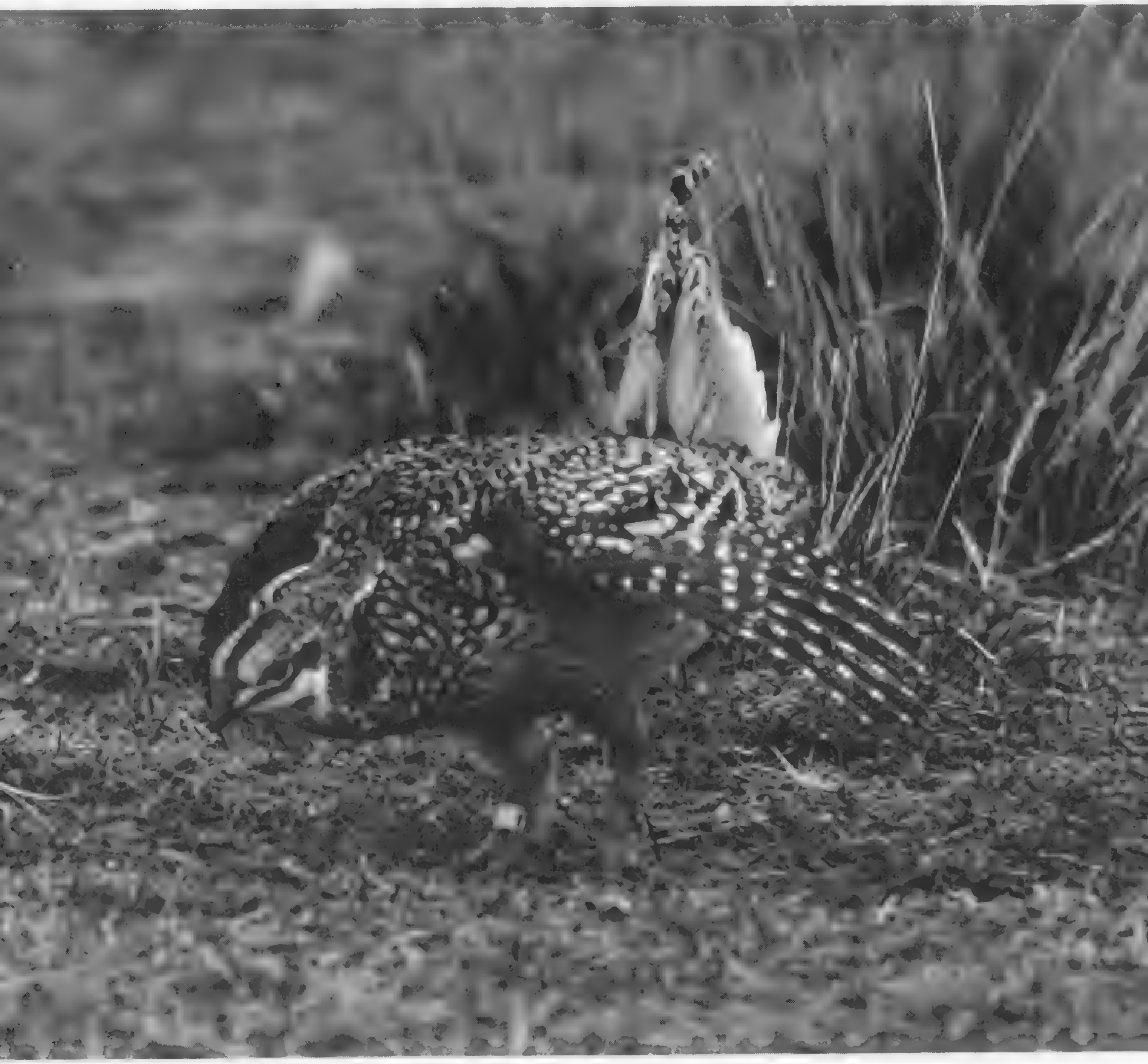

Figure 3. A male Sharp-tailed Grouse, disputing with a rival, shows a white shoulder spot in conjunction with a tail-rattling display. Photograph by the author.

seen males, sitting beside a road, show this spot when I disturbed them. Although female Sage Grouse display the spot occasionally when they are walking on a strutting ground, they most frequently do so while they are gathered in a cluster in a male's territory, when quarreling, and just before copulation (Lumsden, 1968).

Many records of birds showing a shoulder spot lack details of their relationship to other birds in the area. Often there is no description of what the birds did before or after the display. However, when fighting or copulating the bird is clearly in a state of intense conflict. Aggression and fear or motivation of sex and fear are both strong in the bird's mood. In these four species—the Red Grouse, Greater Prairie Chicken, Sharp-tailed Grouse and Sage Grouse—I suggest that the white spot expresses an element of fear in a conflict situation.

The large conspicuous white shoulder patch of the male Black Grouse is composed of feathers that are longer and broader than in most species of grouse and, in fact, seem to be specially modified for a signal function. The dominant males on a lek display the white patch almost continually, particularly during "rookooing" in courtship and in intimidation of other males. Lone rookooing males display the wing spot as much as those in the company of others. Sometimes the spot is less conspicuous just prior to the performance of a flutter-jump and during a fight; it is hidden completely only in alarm. Koivisto (1965) reported that subdominant or "third class" males in Finland often walk about the lek in an upright posture with tails closed and lowered, legs relatively straight, and shoulder patches hidden. Kruijt (1962) noted that in Holland most males on a lek conceal their white markings on the approach of a raptor. He recorded this response when Short-eared Owls (*Asio flammeus*) and Montague's Harriers (*Circus pygargus*) appeared, and even when a Grey Heron (*Ardea cinerea*) flew over. From these observations we can conclude that the shoulder patch of the male Black Grouse expresses aggression rather than fear.

Adjacent to the shoulder the females of the Black Grouse have white feathers with a dark subterminal spot or streak under the patagium. They also occasionally display a white shoulder spot, but not in the same circumstances as males. I have seen female Black Grouse in Scotland expose their shoulder spot only prior to copulation, at a time when there is acute conflict between fear and the sex drive. In Figure 5 a hen showing a white spot returns to her nest to brood. The photographer, Mr. Eric Hosking, reported (pers. commun.) that the blind from which he took this picture had been in position for some days and the female must have become accustomed to it. He did though do some last minute "gardening" to expose the nest better for photography. Very likely this change in the vegetation caused a fear reaction. It was brief, however, and the bird soon settled down on the nest to incubate the eggs. In subsequent photographs she settled on the eggs with a reduced shoulder spot and finally incubated with the shoulder spot completely hidden.

In female Black Grouse, then, this display seems to express the fear component in a conflict situation while in males it expresses aggression. Thus the function of this display is different in each sex of the species.

We know nothing of the function of the shoulder spot in male Caucasian Black Grouse (*Lyrurus mlokosiewiczi*) which occupies a restricted range above

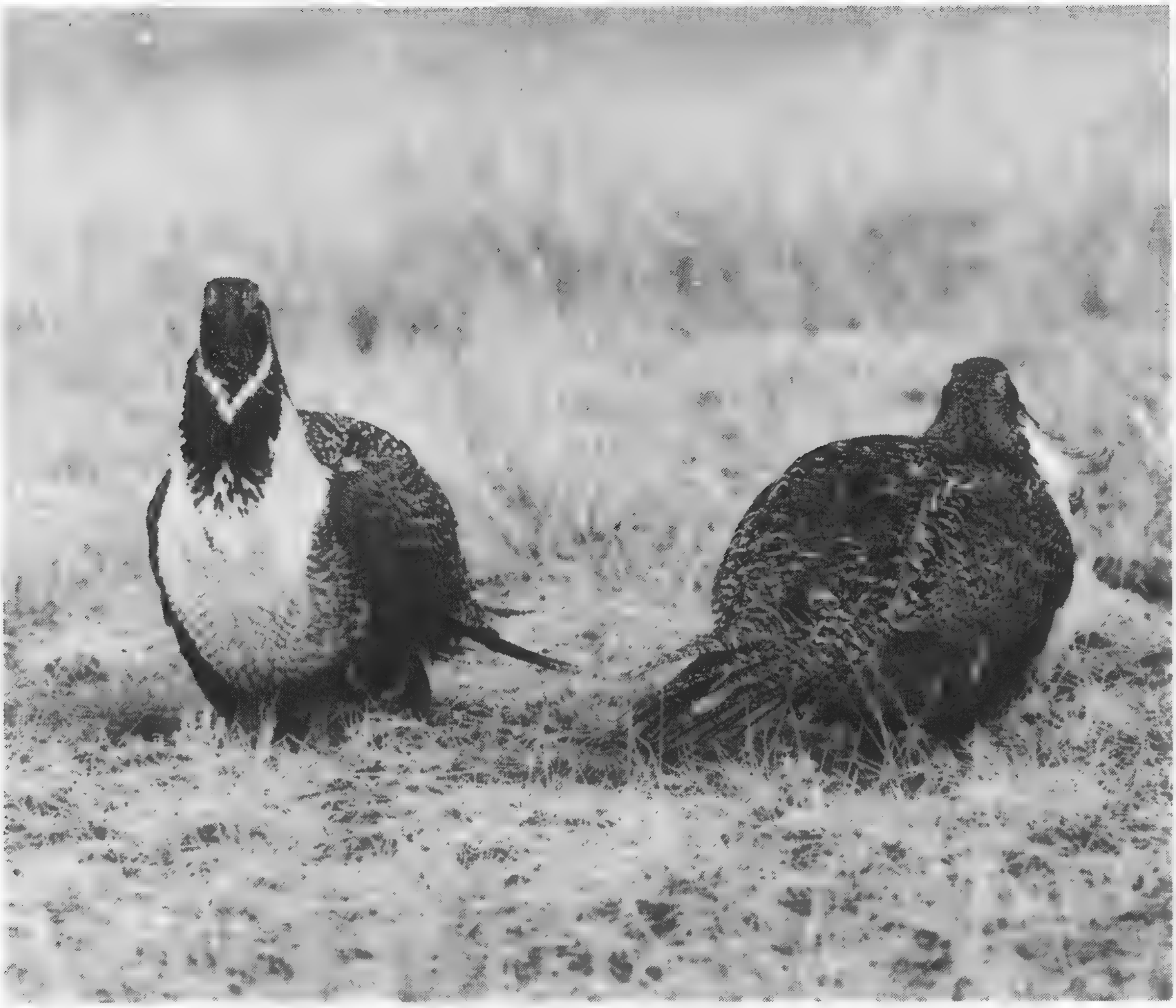

Figure 4. The two male Sage Grouse are in fighting alignment. The subdominant bird on the left reveals his status by his more sleeked upright posture and the white shoulder spot. Photograph by the author.

timberline in the Caucasus Mountains. Lorenz (1887) published a plate of a displaying male with a prominent white patch. In the specimens I have examined the relevant feathers seem to be less well developed than in *Lyrurus tetrix*. We have no records of hens ever displaying a shoulder spot.

The shoulder spot of the male Capercaillie is very large, and, like that of the Black Grouse, formed of unusually well-developed feathers. The spots are conspicuous in the "singing," "threat," and "bowing" displays of the male. The male Capercaillie in Figure 6 is about to perform a "bowing forward" display (Lumsden, 1961). Note the size of the shoulder spot compared with those of the other species illustrated in this paper. The birds start their display activities well before dawn in the spring. In the dim light beneath the trees the darkly colored males are nearly invisible except for their huge ivory-green bills and the white shoulder spots. There are occasions on the leks when the human eye can discern only these light markings moving about in the gloom.

On the display grounds, I have watched subdominant yearling males of the Capercaillie adopting submissive postures and being chased by territorial males, but I have never seen a single bird conceal its shoulder spots. More extensive observations may show that they do.

The shoulder-spot feathers of the female Capercaillie are white with a wide, brown, subterminal U-shaped mark and, sometimes, a small buffy patch.

Although I missed detection of a shoulder-spot display by females during my observations in Scotland, I have since seen it in some movie sequences by Mr. T. Suominen. These females, photographed in Finland, exposed their shoulder spots prior to, and during, precopulatory display.

Since the shoulder spot is most prominently displayed in male Capercaillies in agonistic situations, it is likely an expression of aggression and probably serves an additional function of advertising the exact location of the male in the dim, early morning light beneath the trees. In female Capercaillies, as in female Black Grouse, the display of shoulder spots seems to be a manifestation of fear in a precopulatory situation.

The male Stone Capercaillie (*Tetrao parvirostris*) from eastern Siberia possesses a shoulder spot as well developed as that of the more western species; and the female is potentially capable of showing a spot since the relevant feathers are white with brown bars. We have no information, however, on its function in either sex. The Stone Capercaillie male lacks the huge pale ivory-green bill of its western relative but does have prominently white, tear-shaped spots on its upper tail coverts and on its back. As in the western Capercaillie, these white marks probably act as "flags," advertising the bird's location during display in the dim light beneath the trees.

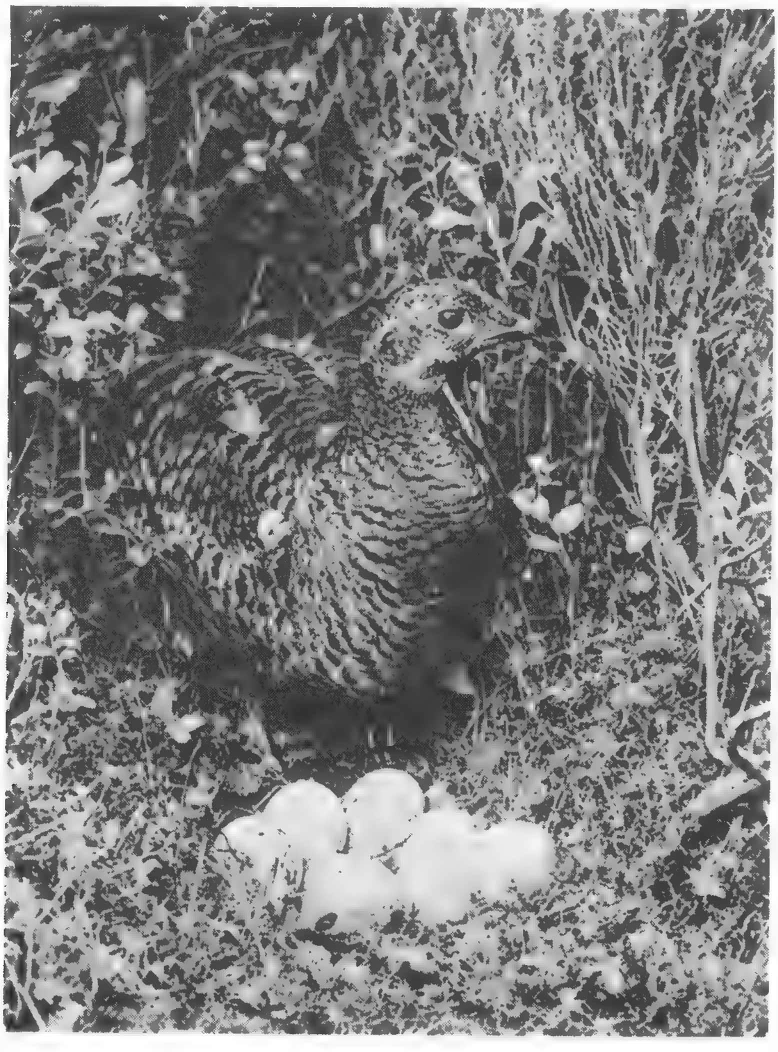

Figure 5. The female Black Grouse betrays her anxiety by her white shoulder spot as she approaches her eggs to brood. Photograph by Eric Hosking.

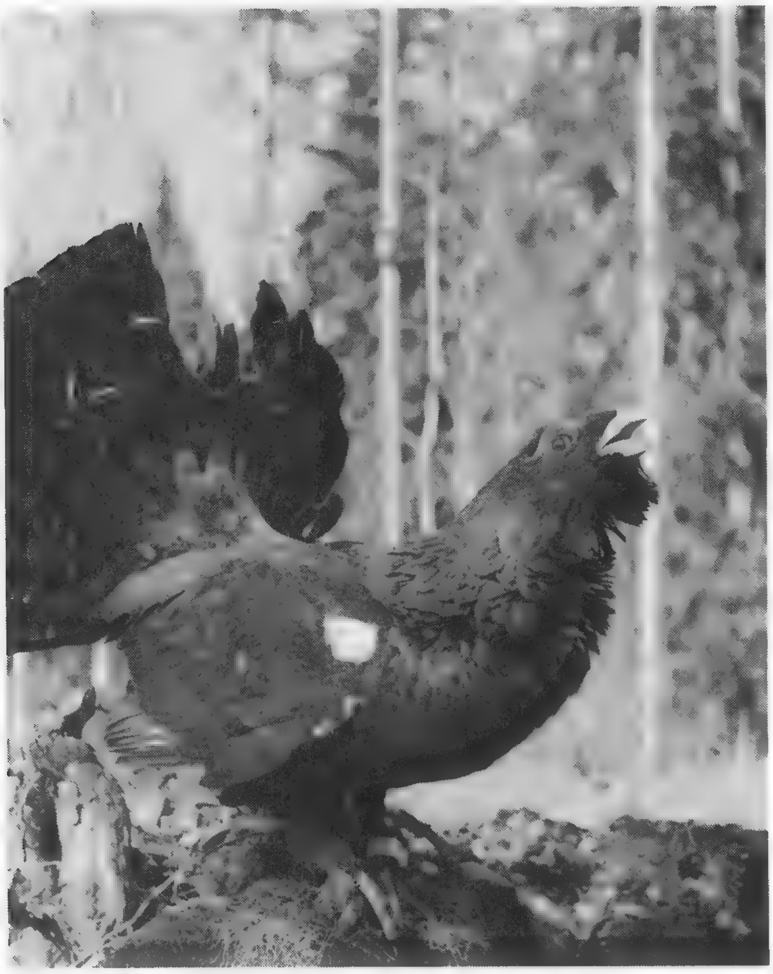

Figure 6. An aggressive male Capercaillie performing his Bowing Forward threat display and showing his prominent white shoulder spot. Photograph by the author.

Although the underwing coverts of both sexes of the Spruce Grouse (*Canachites canadensis*) are largely gray, those beneath the proximal end of the patagium are tipped with white. I made a short movie sequence of a strutting male displaying a small but conspicuous white shoulder spot. This bird, very tame, was being used for a series of behavioral experiments involving both male and female mounts when the movie sequence was taken. I think it likely that fear, caused by lack of response from the mounted specimens and my presence with the camera, may have been responsible for the shoulder-spot display in this bird. I believe that, in addition to the aggressive and sexual displays, fear was also present in his mood and the shoulder spot expressed it. I have not yet seen a female Spruce Grouse perform this display. The Sharp-winged Grouse (*Falcipennis falcipennis*) of Siberia has the same proximal underwing coverts—gray and white-tipped—as the Spruce Grouse and presumably the same capability for display of a shoulder spot. Whether it ever shows the spot is unknown.

According to Mr. S. D. MacDonald (pers. commun.), aggressive male Blue Grouse (*Dendragapus obscurus richardsonii*) always display the shoulder spot prior to and while attacking and fighting their image in a mirror. One male occasionally displayed the shoulder spot during the courtship approach, at a time when the colored skin patches of the neck were exposed and the surrounding white rosette was fully flared. All other males studied, however, failed to show the shoulder spots during courtship. The only female that showed the spot did so in response to the peeping of a newly hatched chick that was caught. Mr. A. N. Lance (pers. commun.) also recorded the shoulder spot display in both sexes of *Dendragapus obscurus fuliginosus.* These observations suggest that the shoulder-spot display in Blue Grouse may express fear in conflict with other behavioral moods. We need more information to confirm this.

No shoulder-spot display has been recorded in the Hazel Grouse (*Tetrastes bonasia*). The largely white coloring of the underwing coverts certainly suggests a potentiality for the shoulder-spot display. The Hazel Grouse male, however, in mature plumage has a broad white bar on each side of the neck extending to the shoulder. This is present but less distinct in females. A white spot adjacent to this white bar would lack the contrast which makes the spot so easily seen in other species, and could, therefore, weaken its function in communication.

The proximal underwing coverts of the Ruffed Grouse (*Bonasa umbellus*) are gray with a variable amount of white tipping. I have not seen or heard of a white shoulder spot displayed by either captive or wild birds of this species.

Conclusion

The shoulder-spot display of grouse seems likely to have originated from a flight intention movement in which the carpal, or wrist, joint was lowered and the wing was removed from the covering of the contour feathers of the body. The eversion and exposure of the proximal underwing coverts on the patagium may have acquired a signal function of intention to fly away in fear situations. In some species the function of the spot changed to an expression of fear in conflict situations. In other species, such as the Black Grouse and Capercaillie, the white spot in the females retained this function while in the males it grew larger and more conspicuous, becoming an expression of aggression.

In spite of the absence of information on the presence of a shoulder spot display in some species, the wide distribution of this behavior pattern in the Tetraonidae suggests this display may be relatively ancient.

Acknowledgments

I would like to express my gratitude to Mr. Eric Hosking for permission to publish his photograph of the female Black Grouse and to Mr. N. Picozzi for permission to use his photograph of the male Red Grouse.

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ORIENTATION IN GULLS: EFFECT OF DISTANCE, DIRECTION OF RELEASE, AND WIND

WILLIAM E. SOUTHERN

In this study I attempted to determine the role of various environmental parameters in the homing behavior of Ring-billed Gulls (*Larus delawarensis*) and Herring Gulls (*L. argentatus*) nesting in a colony at Rogers City, Presque Isle County, Michigan, during the summers of 1963 and 1964.

The Rogers City colony is unique in the Great Lakes area because of its location on a man-made peninsula projecting from the mainland into Lake Huron (see Pettingill, 1958) at N Lat. 45° 20′ and N Long. 83° 40′. About 800 pairs of Herring Gulls and approximately 4,000 pairs of Ring-billed Gulls inhabited this point during the two seasons.

In our homing trials my assistants and I used 320 adult Ring-billed Gulls, three subadult Ring-bills, 56 juvenile Ring-bills, and 50 Herring Gulls, a total of 429 birds. I have included the results of the juvenile trials in a paper (Southern, 1969a), pertaining to orientation-cage trials with Ring-bill chicks. I have incorporated generalizations from the tracking of 41 Herring Gulls by radio during part or all of their homing trials in this paper. The details of the radio-tracking project and my comments on the effect of solar clues are in other papers (Southern, 1969b; 1970).

We released 49 Ring-bills either in or near the colony, attempting to determine: (1) the accuracy of the techniques we were using to record the return times for non-tracked birds; (2) the effect of our handling on the return rates of the birds; and (3) the likelihood of sighting color-marked gulls within the colony.

We released the experimental gulls under a wide range of climatic conditions, at various times of day and night, in all directions from the colony, adjacent to major topographical features such as large bodies of water, and at different distances from the colony. We made single, double, triple, and multiple releases—up to 10 individuals at one time (Southern, 1969c). Since considerable information was already available from Griffin (1943) and Matthews (1952) on the long-range travel of Herring Gulls, we did not attempt to initiate long-range trials. I decided that shorter trials, up to about 150 miles, would provide considerable data regarding the use of environmental clues, homing success, and general orientation behavior and felt that we should be able to apply these findings to longer flights of the species.

Procedures and Techniques

We captured most of the adult Ring-billed Gulls in a cannon net, a technique described earlier (Southern, 1967), and additional Ring-bills and all of the Herring Gulls with snares. Using a 20- to 40-pound-test fishing line of monofilament nylon, we made a noose about 10 to 12 inches in diameter in one end and placed it around a nest-cup, rock, or other commonly used perch. Then holding the other end of the line we retired to wait for the bird to return. When the gull landed, a quick jerk on the line tightened the noose and secured the bird.

Each gull received a Fish and Wildlife Service band and, for individual recognition, a color mark with alcohol-soluble biological stains. In 1964, each gull was given an intramuscular injection of Equitol from the Jensen-Salsbery Laboratories at the rate of 20 milliliters per kilogram of body weight. When temperatures were below 88°F, this dosage was safe and adequate to immobilize a gull for about two hours. At night or when the temperatures were higher, this amount was occasionally fatal. During transit by automobile to release sites we kept most of the gulls in burlap bags and the rest in ventilated corrugated boxes. The periods of confinement ranged from 20 minutes to eight hours. Long periods of confinement, in spite of the Equitol injections, usually had a noticeable effect on the bird's behavior at the release site and resulted in slow homing or even in apparent lack of homing behavior. Long periods of confinement were usually correlated with long distance trials.

I subjected the circular distribution data, presented under the section "Disappearance Points of Adult Gulls with Relation to Home Direction," Table 2 and Figures 6 and 7 in this paper, to the Rayleigh Test (Batschelet, 1965). This test is used to determine whether an apparent concentration of headings toward a preferred direction is significant or if it is due to chance variation: that is, whether the distribution of the population is uniform or whether it is unimodal — with a preferred direction. Thus, it is a statistical test of "randomness." The null hypothesis states that the population has a uniform distribution, implying that $p = 0$. For each set of data, discussed in this paper, I calculated the mean angle, or vector, of the bird's departure, and used the Rayleigh Test to determine whether or not the mean vector differed significantly from zero at the five-per-cent significance level, designated by the symbol P. If the Test Statistic z of the Rayleigh Test is greater than the critical value of zp at the five-per-cent significance level, the null hypothesis of a uniform distribution is rejected and p is significantly different from zero. This indicates that enough of the directional headings at departure are grouped about the mean to make that particular angle of departure statistically significant. If, however, z is less than zp, the assumption $p = 0$ is consistent with the data and we must conclude that the mean angle is of no significance.

Experimental Results and Discussion

Behavior in Relation to Distance of Release Site from Home

We released 272 Ring-billed Gulls at distances ranging from one to 150 miles from the colony and divided this range into nine categories—1-3 miles; 7-10 miles; etc.—in order to obtain an indication of the effects of distance on homing success. The average success rates for Ring-bills in the nine categories ranged from 40 to 100 per cent (Figure 1). The success rates for 46 Herring Gulls, released between 2 and 125 miles from home ranged from 60 to 100 per cent (Figure 2).

We released 258 Ring-bills at distances greater than 15 miles from the colony and the average homing success for each of the six distance categories, between 16 and 150 miles, ranged from 40 to 78 per cent and averaged 62.5 per cent. The highest success level was in the 26-50 mile category and the lowest in the 126-150 mile (Figure 1). The average success rate for Ring-bills released more than 75 miles from the colony was 13 per cent lower than the mean for individuals released from 16 to 75 miles away. This may indicate that Ring-bills begin to encounter increasing difficulty in orientating at distances of over 75 miles from the home colony. In general, as the distances increased, there was a somewhat gradual decline in the success rates of Ring-bills, and, on the average, the birds that did return were slower.

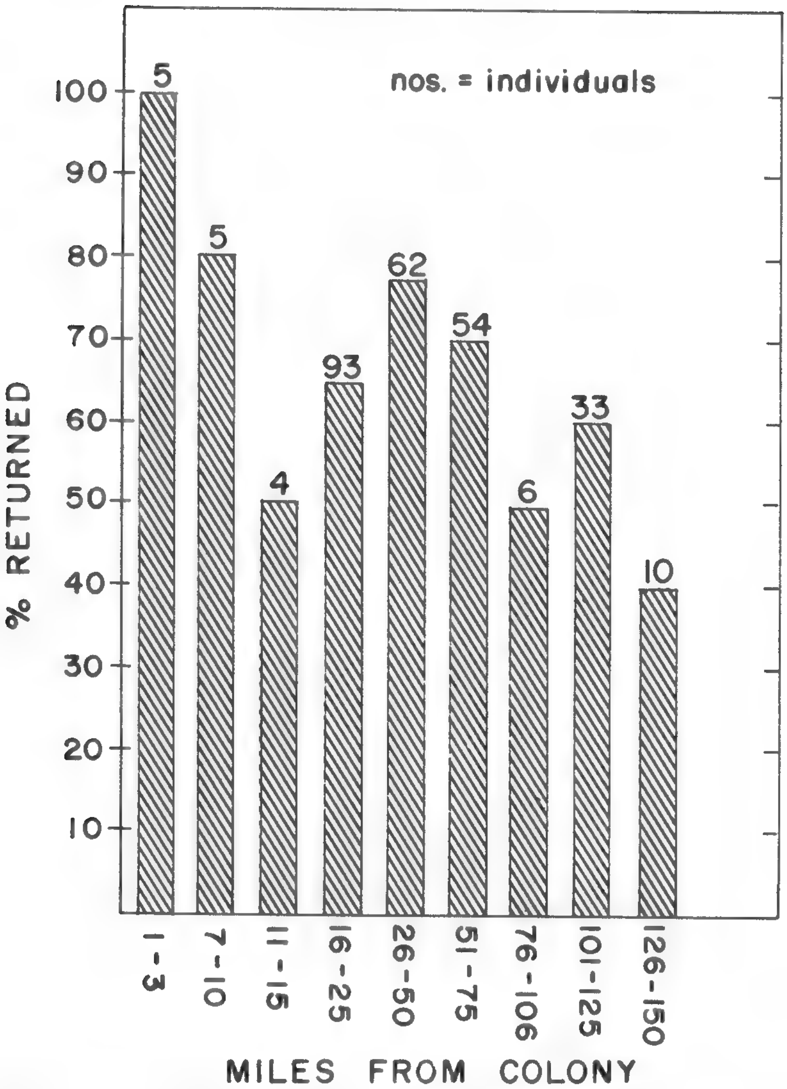


Figure 1. Homing success in relation to distance of release site, Ring-billed Gulls.

The average return rate for 33 Herring Gulls released at distances greater than 15 miles from the colony was 69 per cent (Figure 2). Birds released 101-125 miles away were almost as successful as those released at distances of 26-50 miles. Since most of the categories for Herring Gulls were represented by small samples, it is difficult from these figures to draw sound conclusions regarding their abilities. The data for this species indicate a drop in success after a distance of 10 miles from the colony (Figure 2), but then there was a leveling off and no further decrease occurred. In no instance did the distance of the release site from the colony result in a sharp decline in homing success. The success rate remained above 50 per cent in all but the 125-150 mile category where only 40 per cent of the 10 birds released managed to return. This may suggest the limit of the Herring Gull's efficiency.

Matthews (1952) released 88 European Herring Gulls at distances up to 530 miles and Griffin (1943) released 176 Herring Gulls at distances between 15 and 872 miles. Their data provide an indication of this species' ability to orientate at, and return home from, longer distances. Matthews recorded that 41 per cent of his birds returned but none from distances of over 330 miles. The highest rate of success, 67 per cent, was from distances up to 30 miles; the next highest, 64 per cent, up to 130 miles; and for distances up to 230 and 330 miles, 35 and 34 per cent respectively. The proportion returning showed a general decline as the distances increased.

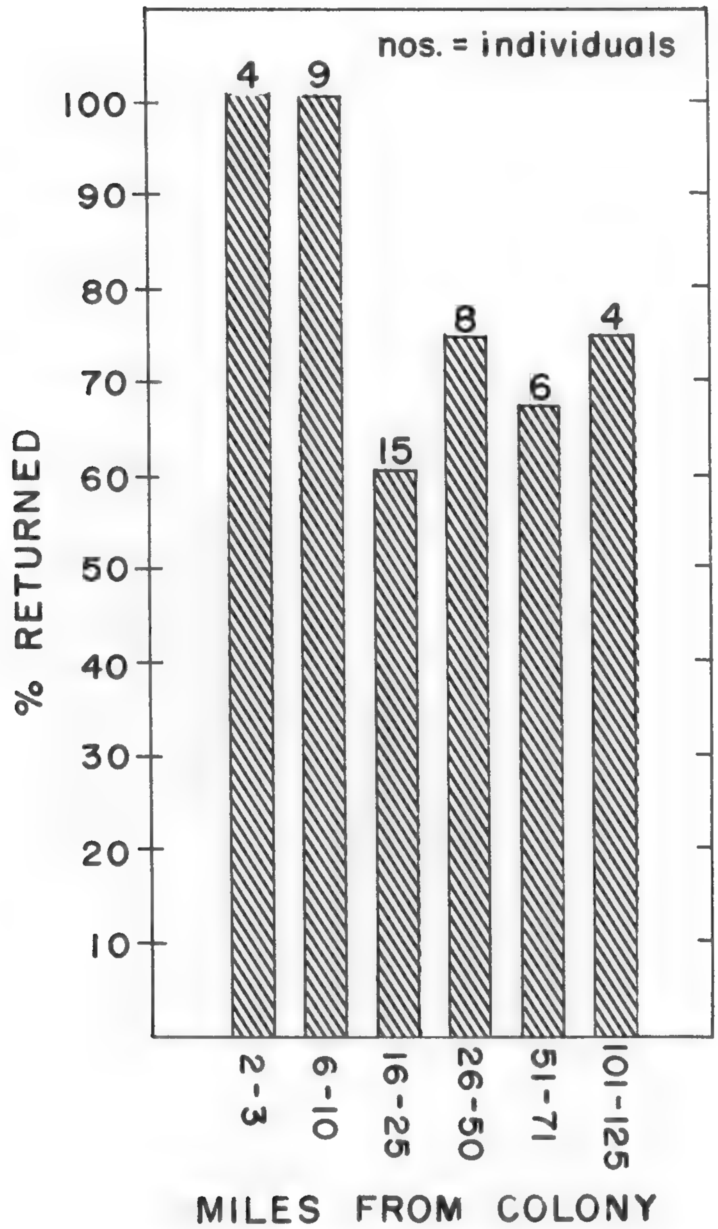


Figure 2. Homing success in relation to distance of release site, Herring Gulls.

Griffin recorded the amazingly high return rate of 93 per cent. The return rates for five individuals released at 870 miles and six at 872 miles were 80 and 67 per cent respectively. The figures of Matthews and Griffin indicate a definite difference between the homing of American and European Herring Gulls. This might be correlated with the difference in their migratory habits, the American form appearing to be more migratory.

It seems as though Griffin's Atlantic Coast birds also homed more successfully than the Herring Gulls on the Great Lakes. Possibly this—if correct—is because the gulls on the Atlantic Coast have larger feeding ranges, or home ranges, than those on the Great Lakes. To my knowledge, we have no evidence to support such a speculation, but the size of the feeding range may explain the significant variation.

Matthews (1952) did not interpret the occurrence of reduced returns with the increase in distance as indicating that the birds found their way home by random exploration or radial scatter from the release point. He thought that a similar decline might occur even if the birds were capable of navigating and speculated that most Herring Gulls home by exploration and are, therefore, rapidly eliminated with increasing distance. However, the increased distance from known landmarks does not affect individuals having a homing method.

After obtaining familiar area estimates from banding data, Matthews released 13 Herring Gulls in "known areas," 30 to 230 miles from the colony and 14 in "unfamiliar areas" the same distance away. The return rates were 77 and 57 per cent respectively. I agree with Matthews that the rather constant levels of homing success suggest the presence of orientational methods other than simple random search for landmarks. I do not agree, however, that the only alternative is navigation as suggested by Griffin (1955) for Type III homing.

Existing evidence supports the contention that Ring-billed and Herring Gulls possess a mode of orientation enabling them to home from long distances. The method involved is not highly accurate or uniform enough to permit most individuals to return rapidly. We found considerable individual variation with good, average, and poor homers. Even the good, the fastest, homers returned much more slowly than we had expected. Their delay might have been because of delayed departures from the release sites or because of some interference with their motivation by the experimental procedures. Perhaps the duress, experienced by the experimental birds, affects their desire to home so severely that it nullifies the value of the homing experiment as a test of orientational ability.

It is important to note that there was no set distance where the success rate dropped drastically. Apparently, whenever the samples were large enough, about 50 per cent of the birds were capable of returning from trials at distances of over 25 miles. In these experiments the distances were not extreme and perhaps a significant percentage of the gulls found their way back to the colony without the use of elaborate navigational techniques. Matthews' (1952) results appear to support this possibility for distances ranging up to 330 miles. Systematic searches for familiar landmarks possibly combined with a type of compass orientation could result in similar success levels.

In general the return speeds were slow. The fastest average speed for any one individual was 19 miles per hour in a 21-mile journey. A radio-tracked Herring Gull averaged 30 mph during a 60-mile flight, but it reduced its homing speed by resting six hours at the release point before starting for the colony. Obviously the return speeds plotted in Figures 3 and 4 do not even approach the average flight speeds of these species. According to Schnell (1965), who measured the speed of gulls from the Rogers City population with a Doppler radar unit, the speeds of Ring-billed Gulls ranged from 11 to 43 mph and those of Herring Gulls from 7 to 43 mph. Both sets of figures include speeds of birds flying with, across, and against winds of various velocities. Thus by maintaining speed near the means of the above speeds—18.8 to 34.7 mph for Herring Gulls flying with and into the wind and 22.7 for Ring-bills—the birds could have traversed even the greatest release distance, 150 miles, in between 4.5 and 8 hours.

Part of the reason for the low average flight speeds is that many of the gulls spent considerable time, perhaps up to six hours or more, "resting" prior to departure from the release sites. We can also conclude that usually the flight paths were not straight lines. Their meandering courses, presumably associated with landmark location, resulted in the birds flying extra miles and further reduced their homing speeds. The radio-tracking of 41 homeward flights showed that about 97 per cent were erratic or meandering (Southern, 1970). The existence of these unmeasurable variables explains why we cannot accept homing speeds as accurate indicators of the bird's ability. Nevertheless, the figures do indicate something about the behavioral sequences associated with homing flights and therefore possibly with migration.

Figure 3 illustrates the homing rates of both Ring-billed and Herring Gulls released at distances greater than 50 miles from the colony. For the birds, homing from distances greater than 60 miles, the rates are quite similar in the first 30 hours. After 30 hours the variation in the rates of return increased. The poorest return speed as well as the lowest success rate was for the 119-150 mile group, all of which were released in Canada on the north shore of Lake Superior. They all flew toward the lake and seemed to follow the shoreline, many of them to the north and west. We noted in several other instances that lake shorelines appeared to serve as false clues and that birds followed them for some distance. The shore of Lake Superior may have been a false clue for the northern group. Unfortunately I could not radio-track these gulls because I was unable to operate my equipment in Canada.

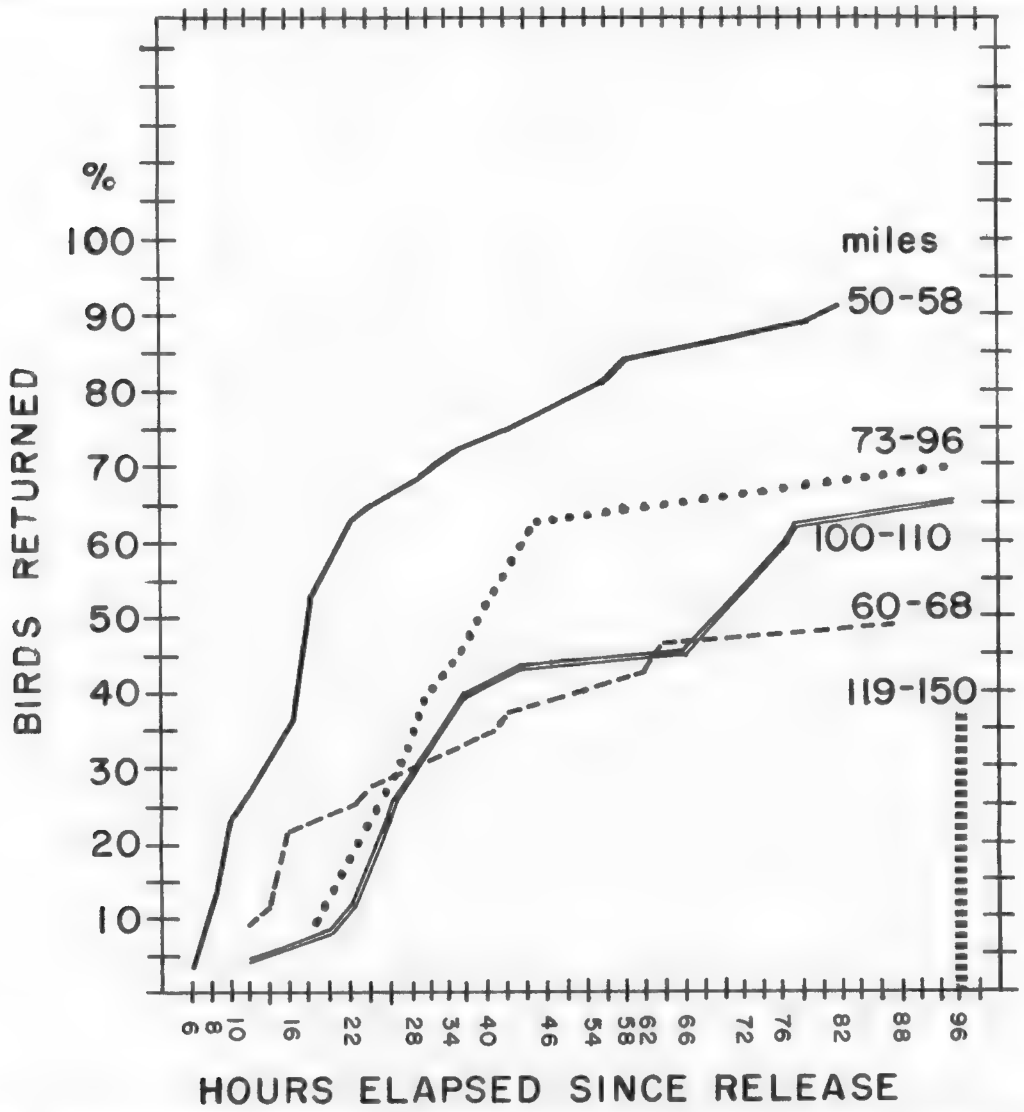


Figure 3. Homing times in relation to distances over 50 miles, Ring-billed and Herring Gulls.

Figure 4 presents similar data for distance groups ranging from one to 47 miles. The number of returns for the three groups that exceeded 10 miles were similar for the first 24 hours; immediately thereafter the returns for the 15-20 mile group slowed down. The other two groups, 23-47 miles, remained similar through 48 hours. In comparing the two graphs we find that there are similarities in the curves of distance groups below 60 miles and in those above and including this figure. The variations within the two groupings are (1) the rapid returns of the 1-10 mile group; (2) the slower returns of the 15 to 20 mile group; and (3) the previously mentioned slow return of the 119-150 mile group. The contributing factors associated with the first and third variations are obvious and need no further discussion. The second variation is rather surprising; I have no satisfactory explanation. Griffin (1943) also mentioned the slow return rates of Herring Gulls from what was considered to be familiar territory.

Matthews (1952) found that at short distances and in known country more than half of the Lesser Black-backed Gulls (*Larus fuscus*) returned very slowly, at less than 20 miles per day. This fraction was radically reduced for releases at greater distances and in unknown areas. Matthews assumed that a proportion of the gulls were homing by random exploration, a procedure that was successful only over short distances and resulted in progressive

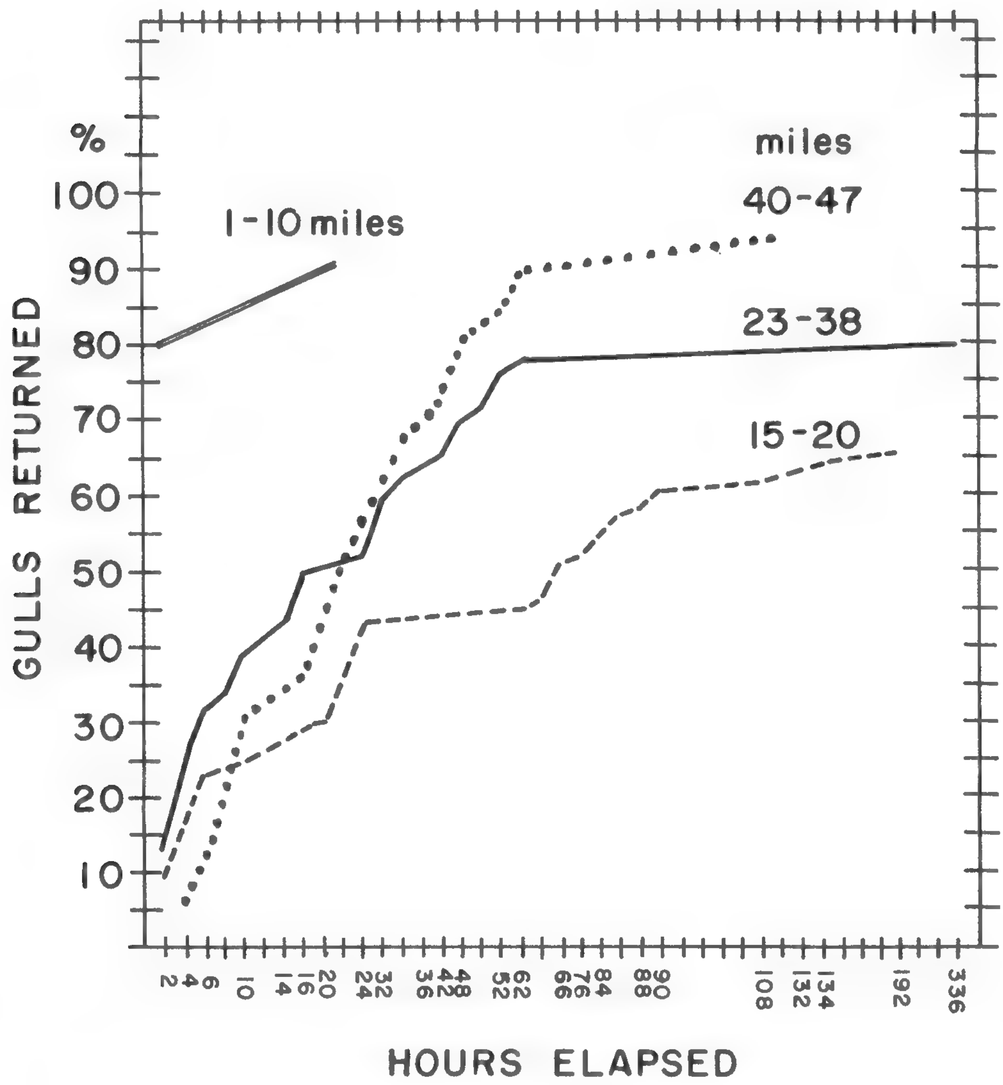


Figure 4. Homing times in relation to distances under 50 miles, Ring-billed and Herring Gulls.

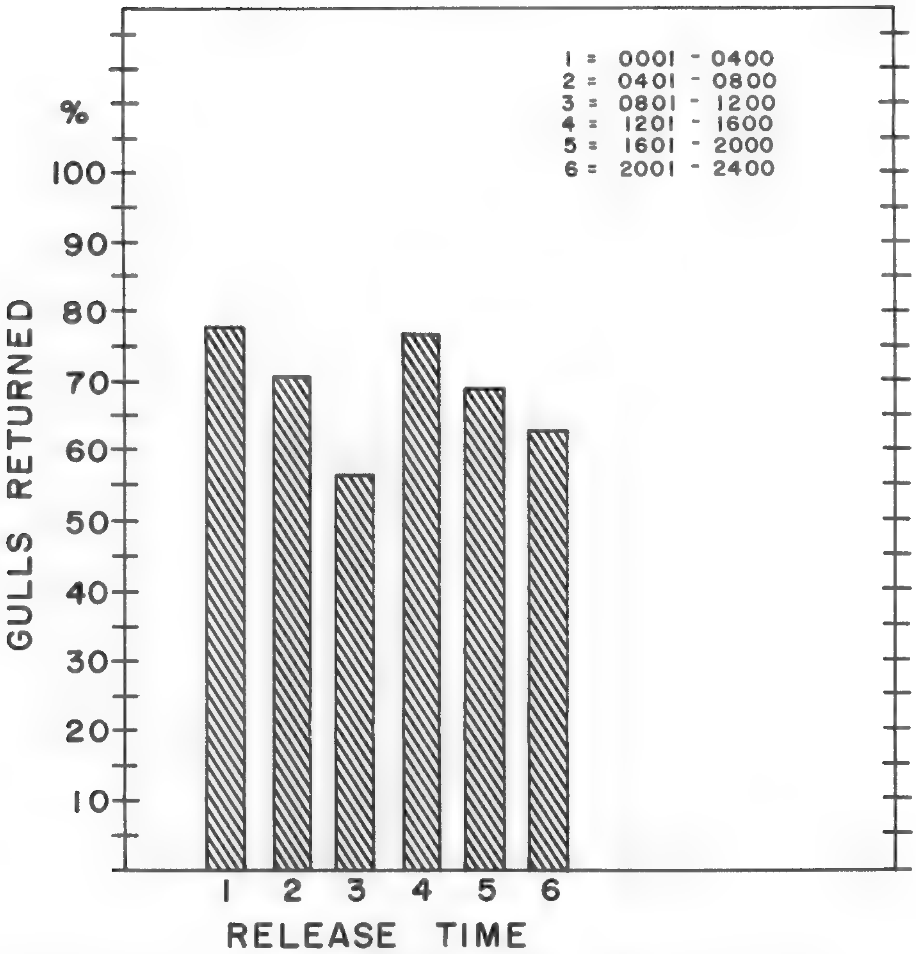


Figure 5. Success rates relative to time of release, Ring-billed and Herring Gulls.

elimination of these individuals as distances increased and familiarity with release areas decreased. The consistency of the proportion of faster returns, at over 60 miles per day, suggested to Matthews that a small fraction of the gulls homed by methods unaffected by distance or the absence of known landmarks. The number of fast Herring Gulls was small, only six per cent, whereas the proportion of very slow returns was high, 68 per cent.

Obviously most Ring-billed and Herring Gulls are slow homers with a fairly wide range of success rates. Indications are that postponed departures from release sites and meandering homeward routes may be partially responsible for the slow returns. Success rates from a variety of distances—up to 872 miles for American Herring Gulls—substantiates the existence of a means of orientation that is adequate for long distance flights as well as short local ones. Homing rates, however, are often surprisingly slow from areas in what should be familiar territory. A discussion of the causes of these variations follows:

Influence of Release Time on Success

I divided the 24-hour day into six four-hour periods—00:01-04:00; 04:01-08:00; etc.—and plotted the average success rate for all gulls released during each of these periods (Figure 5). The birds released during the 08:01-12:00 period had the lowest success rate, 56 per cent; the birds released during periods 00:01-04:00 and 12:01-16:00 had the highest, 77 per cent. The success rates during the remaining periods ranged from 7 to 14 per cent lower than the maximum rate.

TABLE 1

Homing Success and Speed of Gulls with Relation to Release Times

Miles from colony	Time Period 1 00:01–04:00 Number released	Per cent success	Average speed (mph)	Time Period 2 04:01–08:00 Number released	Per cent success	Average speed (mph)	Time Period 3 08:01–12:00 Number released	Per cent success	Average speed (mph)
1–10	—	—	—	—	—	—	—	—	—
15–20	—	—	—	15	65	1.98	31	45	4.85
22–50	13	77	2.3	5	100	1.26	3	100	8.86
53–75	—	—	—	2	75	2.84	14	67	2.19
82–100	—	—	—	—	—	—	3	33	4.97
105–150	—	—	—	—	—	—	3	33	1.51

Miles from colony	Time Period 4 12:01–16:00 Number released	Per cent success	Average speed (mph)	Time Period 5 16:01–20:00 Number released	Per cent success	Average speed (mph)	Time Period 6 20:01–24:00 Number released	Per cent success	Average speed (mph)
1–10	8	88	9.9	2	100	3.0	—	—	—
15–20	27	74	3.22	16	50	0.23	—	—	—
22–50	29	85	4.76	5	100	6.42	19	84	2.66
53–75	5	75	2.79	22	63	2.83	6	67	2.97
82–100	2	100	2.96	—	—	—	8	64	3.79
105–150	25	70	2.05	—	—	—	8	25	2.08

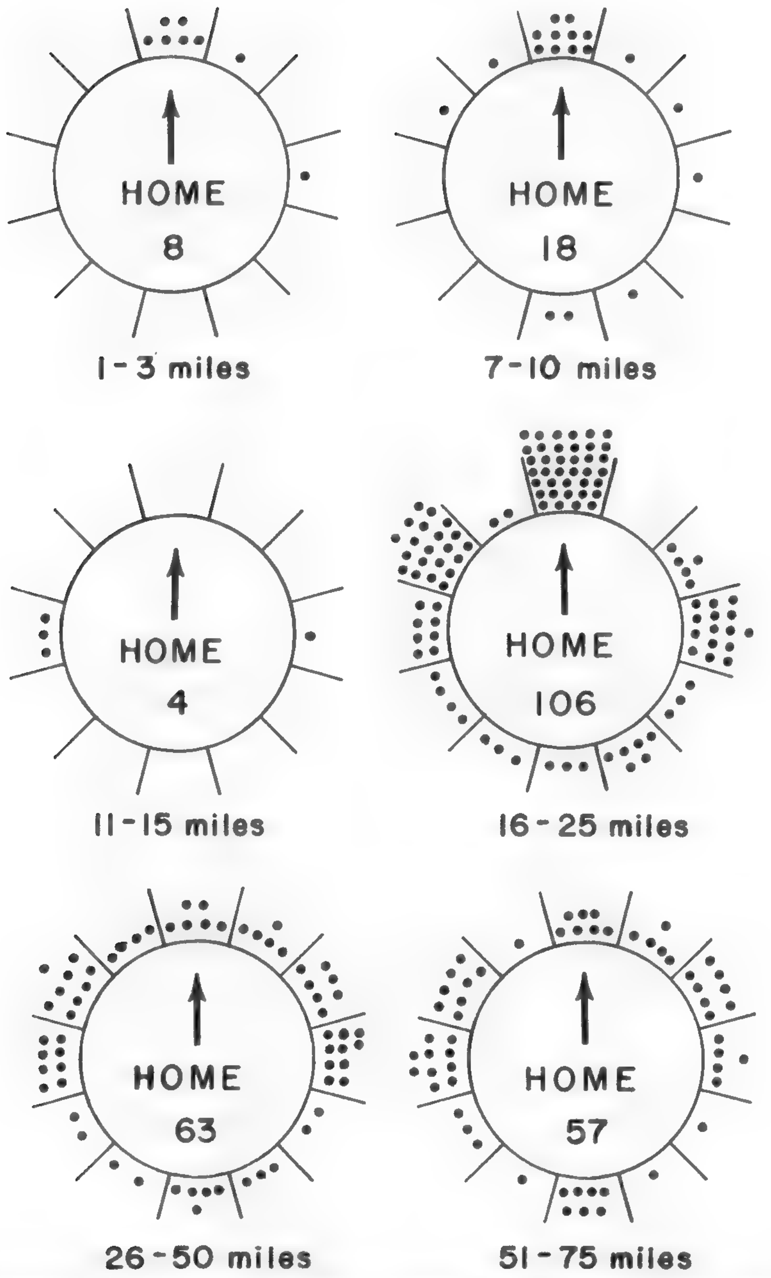


Figure 6. Disappearance points for adult gulls released 1 to 75 miles from home.

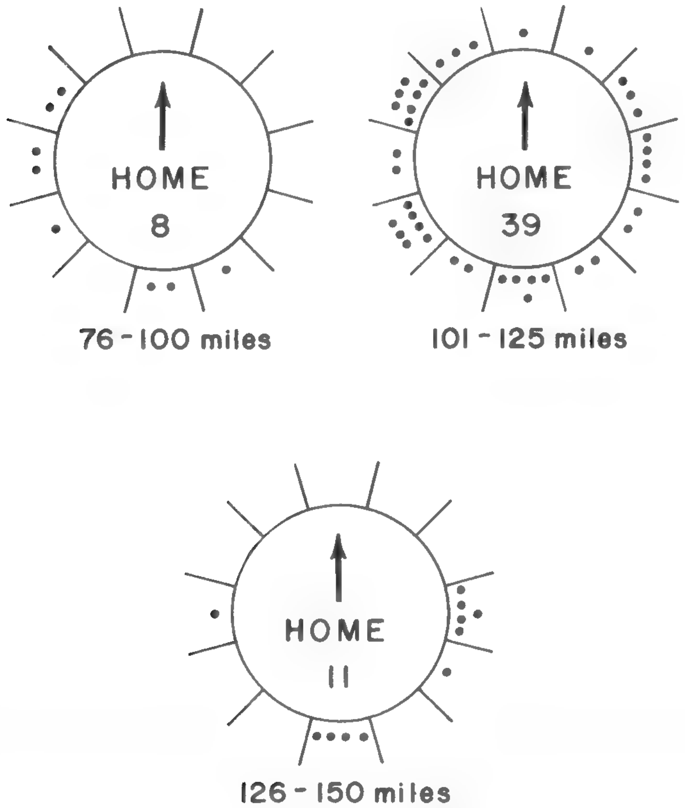
Birds released at night returned as successfully as those released during the daylight periods. Very likely the night-released birds refrained from homeward travel or other orientational flights until daylight. The results from radio-tracked Herring Gulls supported this possibility. None of the individuals that we tracked returned the night of their release, and most, if not all of them, spent considerable time in activities other than flight. Even so, the homing speeds of the birds released at night fell well within the range of the speeds of birds released during the day. Because some birds, released during the daylight hours, devoted varying lengths of time "resting" before starting off, both groups had similar homing speeds. Although the homing speeds of both groups were similar in the end, the postponement of homeward flight until daylight may indicate an inability to orient under nocturnal conditions.

A comparison of homing speeds and success for each of the distance groups with the time period when the release occurred (Table 1) indicates no clear-cut relationship between release time and homing success. Considerable variation in the success rates occurred within particular time periods, particularly in Periods 3 and 6. The average speed and success rates for nocturnal releases were comparable with those for the daylight releases. Possibly the slow homing rates have been the result of individuals searching for landmarks, or, at least, homing by indirect routes. Direct observation and radio-tracking seemed to substantiate both of these possibilities. Strangely, the return times, or average speeds, for the daylight releases failed to vary more drastically from those for nocturnal releases. Tracking data and direct observation indicated that homing birds do not return at night. It may be that the remainder of the night—after release—corresponds approximately to the amount of time many gulls spend resting before departing from release areas. The result is that both groups home at approximately the same range of speeds.

Disappearance Points of Adult Gulls with Relation to Home Direction

The disappearance points of the experimental gulls were grouped into nine distance categories—1-3 miles; 7-10 miles; etc. In each of these categories I have included data from birds released at different sites and data from radio-tracked individuals that we observed visually from the time they were released until they disappeared. I have plotted 316 departure headings (Figures 6 and 7) and listed the mean departure angles and the results of the Rayleigh Test (Table 2).

All but two of the eight individuals released at 1-3 miles were headed in a homeward direction ($\bar{x}$ angle, 102.32°; home = 90°) when last seen. In these instances, it was usually possible to watch the bird's flight behavior while it



76 - 100 miles

101 - 125 miles

126 - 150 miles

Figure 7. Disappearance points for adult gulls released 76 to 150 miles from home.

TABLE 2

Mean Departure Angles and Rayleigh Test Results for Adult Gulls Released at Various Distances from the Colony

Distance category in miles	*Number of trials*	*Mean angle of departure* ($\bar{x}$)	*Standard deviation* (s)	*Test statistic* (z)	P = 5%
1–3	8	102.32	28.25	7.03	2.90
7–10	18	93.87	54.22	5.18	2.95
11–15	4	0.00	57.30	1.00	2.85
16–25	108	79.36	64.72	14.16	3.00
26–50	63	102.23	73.94	1.79	3.00
51–75	57	63.44	73.12	1.96	3.00
76–100	8	330.00	51.79	2.80	2.90
101–125	39	332.75	72.66	1.50	3.00
126–150	11	222.76	51.09	3.99	2.93

was on its way to the colony or until it landed in the water. Gulls that headed inland were more difficult to follow and after a few minutes usually disappeared behind trees or hills. We released two birds that did not angle for home during fog cover. One headed in a direction about 90° removed from the colony (Figure 6); the second paralleled the shoreline and then angled out over the woodlands to the west.

Of 18 gulls, released 7-10 miles from home, 10, or 55.6 per cent, were heading in a homeward direction ($\bar{x}$ angle, 93.87°; home = 90°) when last seen. The remaining eight birds scattered widely over the face of the compass. Three of these returned home within one hour; four between 16 and 22 hours; and one failed to return. Apparently this distance category fell within the normal feeding range of the population, and a departure direction not initially orientated toward home usually resulted in homing rates slower than those for birds initially selecting a homeward bearing. In this 7-10 mile category, 63 per cent of the releases that showed aberrant headings were slow in returning or failed to return.

Of the four birds released at distances of 11-15 miles, two returned but required 65 and 66.5 hours to do so. The mean departure angle, 0.00°, is not significant for this group. At shorter distances the birds either found familar landmarks more readily, reached the shoreline and followed it, or saw the colony when they had gained sufficient altitude.

I believe the behavior of the 108 gulls released at the 16-25 mile category suggests an inability to locate familiar landmarks immediately. Very likely all birds from the colony do not use identical feeding areas or travel the same routes thereto. Only 35.2 per cent of this group selected a departure direction ($\bar{x}$ angle, 79.35°; home = 90°) suggestive of a homeward tendency. We should note that many, 61.1 per cent, of the releases selected a direction included in the "hemisphere," approximately 150°, centered on home. In this hemisphere group 65 per cent of the Ring-bills and 60 per cent of the Herring Gulls returned. Of those departing in directions included in the opposite hemisphere, 35 per cent returned. The mean angle of 79.3° tested significant at the five-per-cent level (Table 2).

In the next three categories—26-50, 51-75, and 76-100 miles—the homeward headings decrease and the randomness increases. In each category we lack mean departure headings that are statistically significant. The fact that only 10.8 per cent of the gulls, released at 26-75 miles, departed on a homeward course suggests that the method of orientation, used by these species after displacement from the colony, is less efficient at distances over 25 miles.

In the 126-150 mile category we find a continued tendency for the gulls to depart in other than a homeward direction. The mean departure angle of 222.76° is, according to the tests, significant at the five-per-cent confidence level (see Table 2). Although there is a significant directional preference indicated for this category, the mean angle is far removed from an acceptable homeward course. A possible explanation for the apparent significance of this non-homeward course is that this particular mean angle is an artifact resulting from the directional headings of this release category being clustered into essentially two groups. Such groupings of data points represent a bimodal distribution for which the Rayleigh Test is inappropriate (see Batschelet, 1965).

On the basis of these data, it appears that to an adult gull a locality more than 25 miles from the colony is unfamiliar—an area where landmarks are not readily recognizable—and the bird must use other, and perhaps less efficient, orientation methods to return to a known area.

Effects of Direction of Release Site from Colony on Homing Success

We determined homing results for 271 Ring-billed Gulls, released at nine different compass directions from the colony, and for 48 Herring Gulls released at six different directions. Because we had no boats suitable for travel on Lake Huron, we released no birds over the water east and northeast of the colony. In analyzing the data I attempted to determine what effect, if any, the direction of the release site had on the homing success. Table 3 summarizes the Ring-billed Gull data and Figure 8 gives the average success rates of this species. Table 4 and Figure 9 present similar data for the Herring Gulls.

The Ring-bills released to the west-northwest of the colony had the lowest average success rate, 44 per cent; those to the north the second lowest, 59 per cent. In both instances the most distant releases were made adjacent to Lakes Michigan and Superior where, as mentioned previously, the shorelines seemed to provide false clues and the gulls usually followed the shoreline regardless of its direction from the home colony. This type of positive response to such topographical features often resulted in low average return rates for the birds involved.

The lowest Herring Gull success rate, 33 per cent, was for the group released southwest of the colony. However, the sample is too small to indicate increased orientational difficulties from this direction. All of the Herring Gulls released at sites north of the colony returned. We may correlate this with experiences acquired during juvenile dispersal in these northern areas (Southern, 1968).

TABLE 3

Success Rates of Ring-billed Gulls Released at Particular Directions and at Various Distances from the Colony

Direction of release site from colony	*Number released*	*Range of distances (miles)*	*Per cent of total returned*
North	22	2–58	59
North-northwest	45	53–152	64
Northwest	3	75–82	100
West	120	9–50	74
South	8	7–28	63
West-northwest	27	38–110	44
West-southwest	15	40–73	80
Southwest	9	35–53	78
South-southwest	22	60–68	64

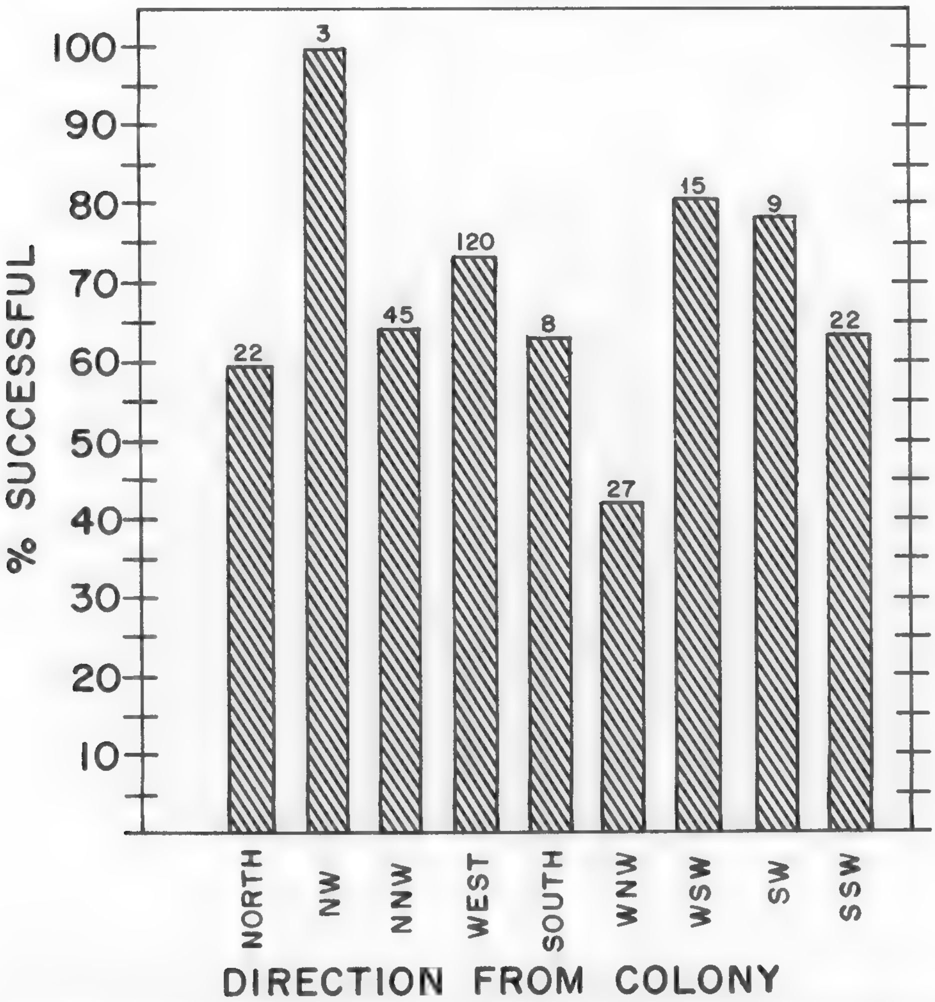


Figure 8. Average success rates for Ring-billed Gulls released at various directions from the colony.

TABLE 4

Success Rates of Herring Gulls Released at Particular Directions and at Various Distances from the Colony

Direction of release site from colony	*Number released*	*Range of distances (miles)*	*Per cent of total returned*
North	5	2–105	100
Northwest	3	110	67
West	26	9–60	77
West-northwest	9	38–110	78
West-southwest	2	73	100
Southwest	3	47–55	33

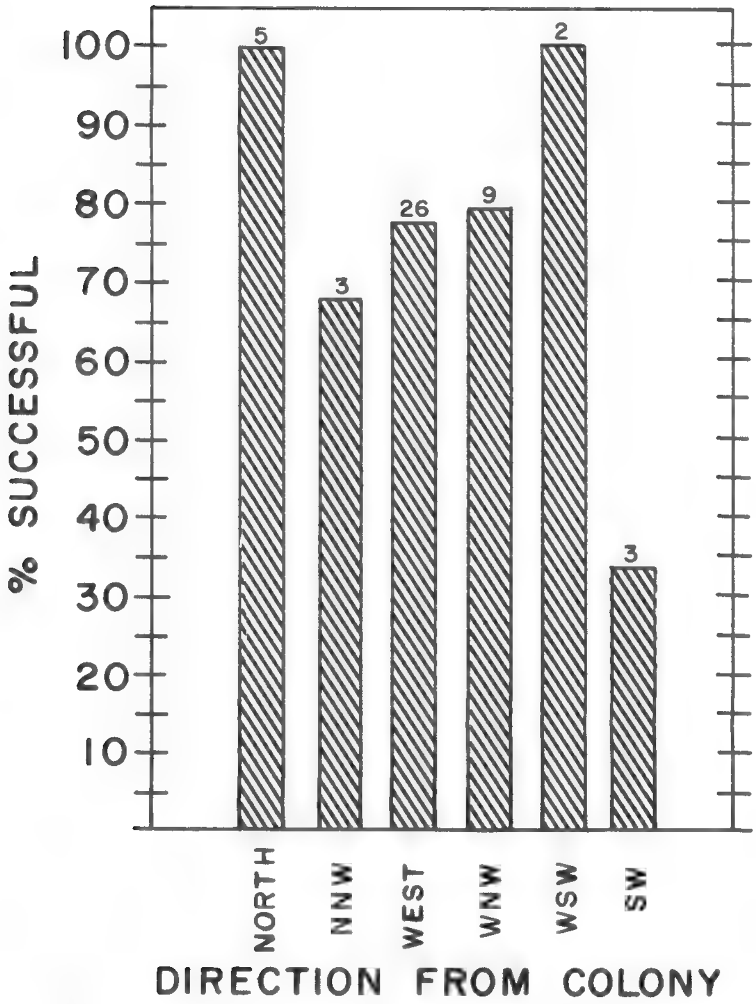


Figure 9. Average success rates for Herring Gulls released at various directions from the colony.

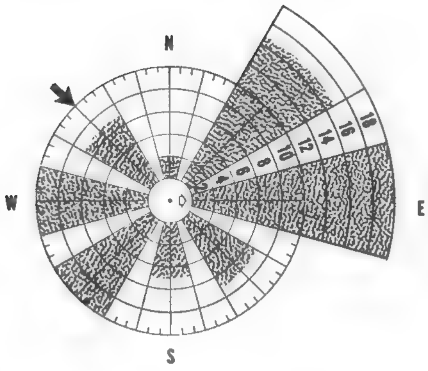


Figure 10. Departure directions with reference to wind direction: All releases over 15 miles from the colony during northwest winds (indicated by the solid arrow). Numerals = the number of gulls released; open arrow in center = the direction to the home colony.

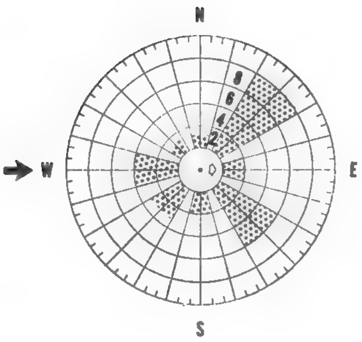


Figure 11. Departure directions with reference to wind direction: All releases over 15 miles from the colony during west winds.

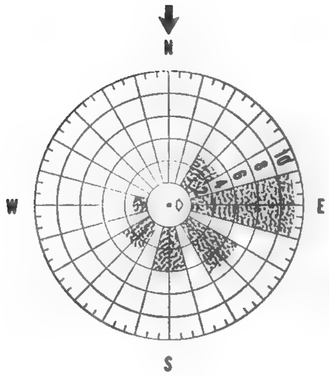


Figure 12. Departure directions with reference to wind direction: All releases over 15 miles from the colony during north winds.

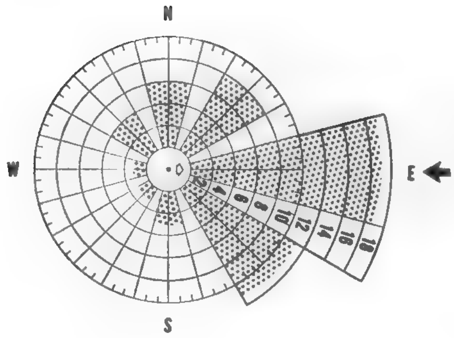


Figure 13. Departure directions with reference to wind direction: All releases over 15 miles from the colony during east winds.

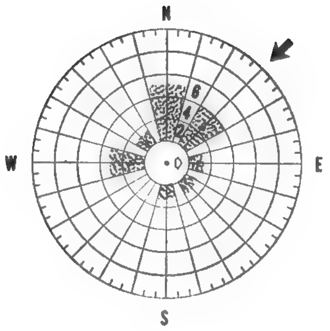


Figure 14. Departure directions with reference to wind direction: All releases over 15 miles from the colony during northeast winds.

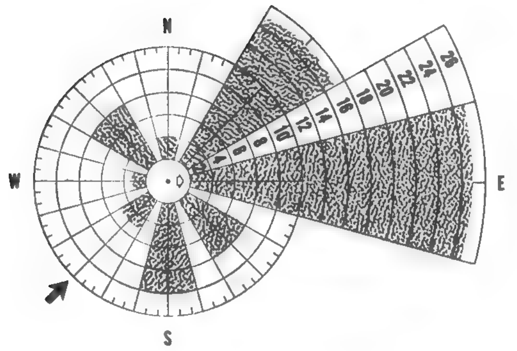


Figure 15. Departure directions with reference to wind direction: All releases over 15 miles from the colony during southwest winds.

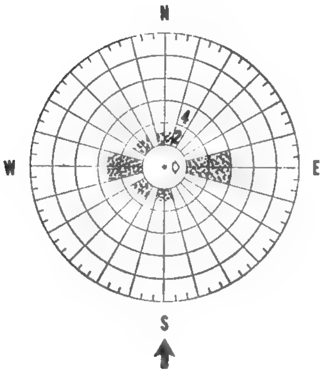


Figure 16. Departure directions with reference to wind direction: All releases over 15 miles from the colony during south winds.

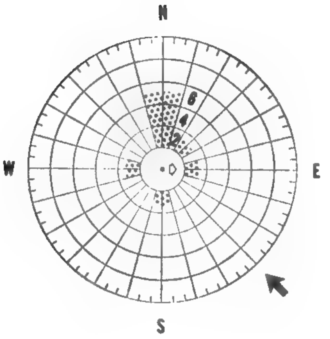


Figure 17. Departure directions with reference to wind direction: All releases over 15 miles from the colony during southeast winds.

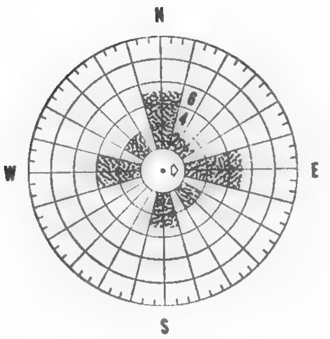


Figure 18. Departure directions with reference to the absence of wind.

There is no clear-cut indication from these data that there is any one direction, or group of directions, from which the Rogers City gulls experience extreme difficulty in orientation. The topographical features, associated with release sites, appear more important to orientation than the direction of the release site from the colony.

The orientation method used by gulls is such that it enables them to home from a variety of compass directions with almost equal levels of success. Possibly gulls never encounter circumstances under natural conditions, such as migration, that would require them to differentiate between the shorelines of Lakes Michigan and Huron. During migration, gulls arrive at the colony by following a known route and observing certain landmarks. Any future flight directions are probably based on a variety of clues, observed near the colony, and not on those that suddenly appear to a bird released along any lake shore. Very likely, we, in conducting these homing experiments, deprive our subjects of a significant portion of the total stimulus normally associated with orientation. As a result, the birds, after release, attempt by wandering flights and other activities to obtain the complex of stimuli necessary for their homeward flight. It seems unlikely that gulls, released beyond immediate view of the colony, select a homeward course, a course to be continued without change, on the basis of any one environmental clue. Apparently some gulls, such as those that were released at northern sites and returned successfully, eventually acquire the necessary information.

Effect of Wind Direction

Departure headings, selected at all release sites, are plotted against wind direction in Figures 10 through 17. In four instances, in winds from the northwest, north, east, and southwest with velocities ranging from 2 to 30 mph, the mean direction chosen in relation to the wind direction was statistically significant (Table 5). The mean angles ranged from 93.26° in an east wind to 129.11° in a north wind and thus the birds, released in winds from these four directions, all traveled southeasterly toward home. Bearings for other wind directions (Table 5) lacked significant mean angles and all but one, the west wind, were in directions far removed from east-southeast. A significant mean heading is also lacking in the data pertaining to releases made during periods of no wind (Figure 18; Table 5).

TABLE 5

Mean Angle of Departure and Rayleigh Test Results for Gulls Released under the Influence of Winds from Various Directions

Wind direction	*Number of trials*	*Mean angle of departure* ($\bar{x}$)	*Standard deviation* (s)	*Test statistic* (z)	P = 5%	*Consult figure in text*
Northwest	74	116.59	72.34	3.05	3.00	10
West	27	127.67	69.69	1.83	3.00	11
North	25	129.11	51.38	8.94	3.00	12
East	51	93.26	58.40	11.77	3.00	13
Northeast	16	11.03	64.89	2.06	2.95	14
Southwest	66	95.65	56.90	16.96	3.00	15
South	11	225.00	79.10	0.02	2.93	16
Southeast	9	10.89	56.77	2.33	2.91	17
No wind	22	32.68	77.06	0.20	2.96	18

When the wind was from the northwest, 54.1 per cent of the gulls showed homeward tendencies—selected the homeward hemisphere of 150°; 59.3 per cent departed in homeward directions with west winds; 68 per cent with north winds; 76 per cent with east winds; 76.7 per cent with southwest winds. The results suggest that gulls may use wind direction in some manner for homeward orientation. With respect to the other wind directions—south, southeast, and northeast—36.4, 22.2, and 37.4 per cent respectively selected easterly courses even though a significant mean angle is not present in the data. During no wind, 36.4 per cent headed into the homeward hemisphere although the overall departure pattern was random. We cannot, at this time, conclude that wind clues are significant, yet we must not overlook the possibility that the birds may use wind direction in combination with one or more other clues.

The use of wind clues in orientation seems logical because migrating birds are likely to respond to winds associated with frontal systems and other climatic factors, and many high flying birds use upper air masses and associated fronts which are apparently more constant as well as cyclic in seasonal appearance. Thus such a possibility is more likely during migration. Orientation by climatic clues would permit gulls to select and maintain a course during migration; landmarks would be used for recognition of familiar areas. Wind direction stands out as a likely aid to orientation and we should investigate it further.

Summary

During the summers of 1963 and 1964, a total of 373 adult and subadult Ring-billed and Herring Gulls (*Larus delawarensis* and *L. argentatus*) were

used in homing trials. The distances of release sites from the colony near Rogers City, Michigan, ranged from 2 to 150 miles.

An increase in distance of release sites from home did not have a drastic effect on success rates. Particular areas, perhaps those most likely to be familiar to birds from this colony, had especially low return rates. Return speeds were usually slow, the fastest averaging 19 miles per hour. Postponed departure from release sites and meandering homeward routes were partially responsible for slow returns. The time or hour of release had no effect, adverse or otherwise, on the homing rates. Gulls released at night usually postponed extensive flights until daylight.

In the homing experiments for 319 gulls released at nine different compass directions from the colony, the Ring-bills released west-northwest of the colony had the lowest average success rate, 44 per cent; and those released north of the colony the second lowest, 59 per cent. In both instances, the most distant releases were adjacent to Lake Michigan or Lake Superior, both of which seemed to provide false topographical clues. The lowest Herring Gull success rate, 33 per cent, was for the southwest group. Generally, there was no single direction from which gulls seemed to experience extreme difficulty in orientation. Topographical features near release sites were more likely to cause adverse effects.

There is a possibility that winds, associated with atmospheric conditions, influenced departures. The gulls departed more readily if conditions were especially suitable for flight. The "worst air conditions" were associated with completely overcast skies. Departure directions selected by gulls experiencing winds, 2 to 30 mph, from four of the eight plotted directions showed homeward preferences that were statistically significant; during periods of no wind, the birds scattered at random. High standard deviations are associated with each set of data.

Acknowledgments

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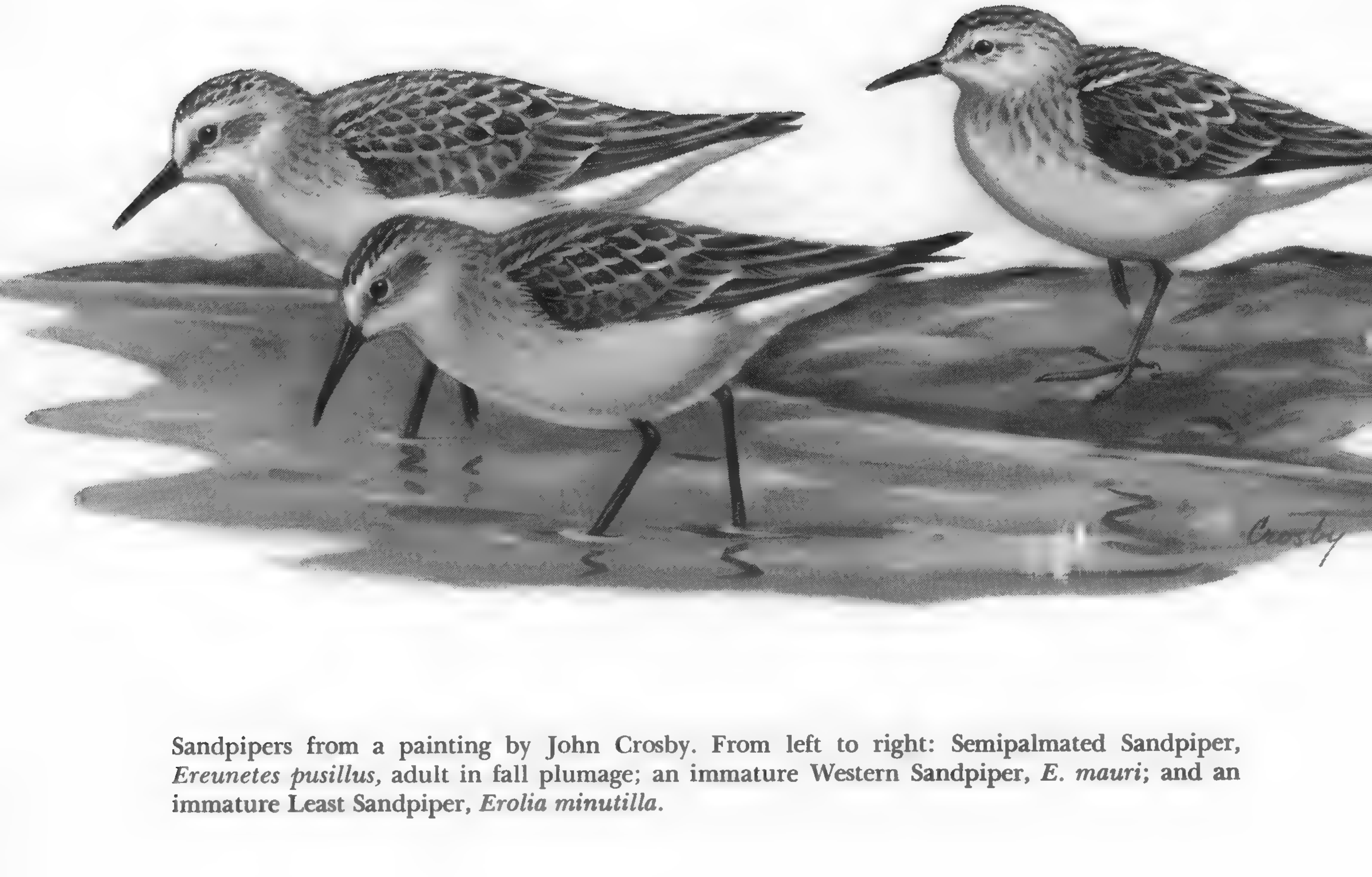


Sandpipers from a painting by John Crosby. From left to right: Semipalmated Sandpiper, *Ereunetes pusillus,* adult in fall plumage; an immature Western Sandpiper, *E. mauri*; and an immature Least Sandpiper, *Erolia minutilla.*

BREEDING BEHAVIOR OF THE SANDERLING IN THE CANADIAN HIGH ARCTIC

DAVID F. PARMELEE

All photographs and black-and-white drawings by the author

The Sanderling (*Crocethia alba*) nests abundantly in the Arctic if we judge by the migration each spring and fall. Yet, despite this, I have found few species more elusive on their breeding ground and none that have intrigued me more. George Miksch Sutton and I failed to find Sanderlings on Baffin Island in 1953; S. D. MacDonald and I recorded only a few on Ellesmere Island and not one on Axel Heiberg Island in 1955. On southeastern Victoria Island and on Jenny Lind Island in Queen Maud Gulf, in 1960, 1962, and 1966, the members of our expedition could not find enough Sanderlings for a detailed study, and there was little consolation in knowing that our few notes were more than were being gathered elsewhere. The fact remained that, until 1968, practically nothing was known of the species' breeding in Canada.

I welcomed the opportunity to join S. D. MacDonald, from 20 May to 13 August 1968 and 7 to 29 June 1969, on the expeditions of the Canadian National Museum of Natural Sciences to Bathurst Island in the Queen Elizabeth Islands, just south of the 76th parallel (Figure 1). Bathurst Island with its distinct location and terrain promised a good Sanderling population, and this proved to be the case though the birds were more thinly scattered than anticipated. Nevertheless, I was able to concentrate on various aspects of the Sanderling's behavior—courtship and mating, pair-bond relationship, and the role of the sexes in the care of the eggs and young.

Information on the Sanderling's breeding, prior to 1968, stems largely from studies in Greenland and Spitsbergen, and most of these, Bannerman (1960) pointed out, date back to Manniche (1910). Though Manniche's work was outstanding for his time and distinctive in being the first useful study of the species, a careful scrutiny reveals many ambiguities, gaps, and flaws. The present study extends our knowledge of this shorebird and will, hopefully, stimulate further research.

Study Areas and Methods

We established our base camp eight miles inland on a prominent, finger-like ridge about halfway between Goodsir and Bracebridge Inlets (Figure 2). The camp ridge, as we called it, extended westward as part of a system of low, barren ridges that continued along the north shore of Bracebridge Inlet (Figure 3). Broad valleys with innumerable marshy ponds and lakes stretched between the two inlets. Goodsir River, the largest stream, flowed from high ground in the northwest to the base of camp ridge, and thence to Goodsir Inlet by a long, meandering route that over the years had left behind many gravel terraces. The varied terrain appeared ideal for Sanderlings.

Originally, in 1968, I planned to select a study area, preferably near camp, where a dozen or more pairs of Sanderlings bred. Not finding such a concentration, I settled on two principal areas — one west of camp and one beyond the stream northeast of camp. The latter, overrun by predators and inaccessible from 9 to 15 July when the stream crested, was an unwise choice.

Because the Sanderling pairs were so thinly scattered over the study areas that we had to cover much ground in checking nests, and because we lost three nests to predators in quick succession, we changed our plan again. Selecting a nest (Nest 2) within half a mile of camp, we erected a blind and kept it under constant surveillance. Thus we protected the nest from predators and, at the same time, collected unparalleled data on a single nest.

We began observation at 15:00 hours on 5 July and continued our surveillance, without a break, until 23:17 on 19 July — after all the young had hatched. Inasmuch as we had observed this nest periodically since 21 June, when it had one egg, the successful hatching of all four eggs had special significance.

We divided the 24 hours of continuous daylight into four, six-hour shifts: MacDonald took the first, 00:00 to 06:00; Cy G. Hampson the second, 06:00 to 12:00; Philip S. Taylor the third, 12:00 to 18:00; and I the fourth, 18:00 to 24:00. Such a division allowed each person time for other studies and gave me the opportunity to check other Sanderling nests and compare them with Nest 2. During critical periods at other nests David R. Gray took over for me at the blind.

The continuous observation at Nest 2 had many advantages. One advantage, perhaps not obvious, was that the incubating bird quickly accepted our presence and behaved as if we did not exist, even when we relieved each other at the blind. Although our coming and going had little visible effect on the bird, it nevertheless quickly responded to all mammals and other birds that approached the nest.

Manniche (1910) observed that once the incubating Sanderling is conditioned to human activities, it soon becomes indifferent to them and sometimes incredibly fearless. This behavior, seen many times in certain tundra sandpipers, appears to be markedly characteristic of the Sanderling, for indeed the incubating birds, with few exceptions, soon became fearless once we found their nest. Our continued presence appeared to steadily increase the fearlessness of the incubating bird at Nest 2. It was so accustomed to us by the time the young hatched that it regularly flew off on routine feeding trips when we knelt beside its young, even when we handled them in plain view. With such fearlessness I feel that our presence influenced or biased the behavior of the bird very little, if at all.

There is no easy way to find a Sanderling nest unless one stumbles upon it accidentally. We observed 11 nests on the Bathurst Island breeding ground in 1968 and three in 1969. We found 12 of these by watching birds that behaved as if they had recently left eggs and only two by systematically dragging ropes over bluffs and ridges. The surest method, it would now seem, would be to watch the feeding areas closely from 06:00 to 18:00 when the incubating birds most often fly from the nest to the feeding ground.

We trapped incubating Sanderlings at the nest in a Myers' trap (1966). The birds appeared not to be overly concerned with the trap and most of them we caught quickly. When the trap partially obstructed their view, certain individuals momentarily lost their ability to locate the nest, and, consequently, ran about looking for it in a disoriented manner. This problem we remedied by allowing the bird to go to the nest with the trap set some little distance away and then gradually moving it closer. Once the bird saw the nest within the trap, it did not hesitate to run across wire and net to its eggs.

We banded the Sanderlings with standard numbered bands provided by the Canadian Wildlife Service, and marked adults with several brightly colored dyes rubbed on various feathers. We found fast drying water-resistant dyes (Dixon Redimark, Joseph Dixon Crucible Company, Jersey City, New Jersey), applied with felt-tip markers, highly satisfactory. In 1968 we banded and color-marked eight adults at eight nests; none of these birds deserted. A ninth adult we caught and marked near its young some distance from the nest. Since only one member, either sex, of the pair incubated and brooded, we caught and marked only one adult for a given nest or brood. How one can catch both members of a pair on the nesting ground prior to incu-

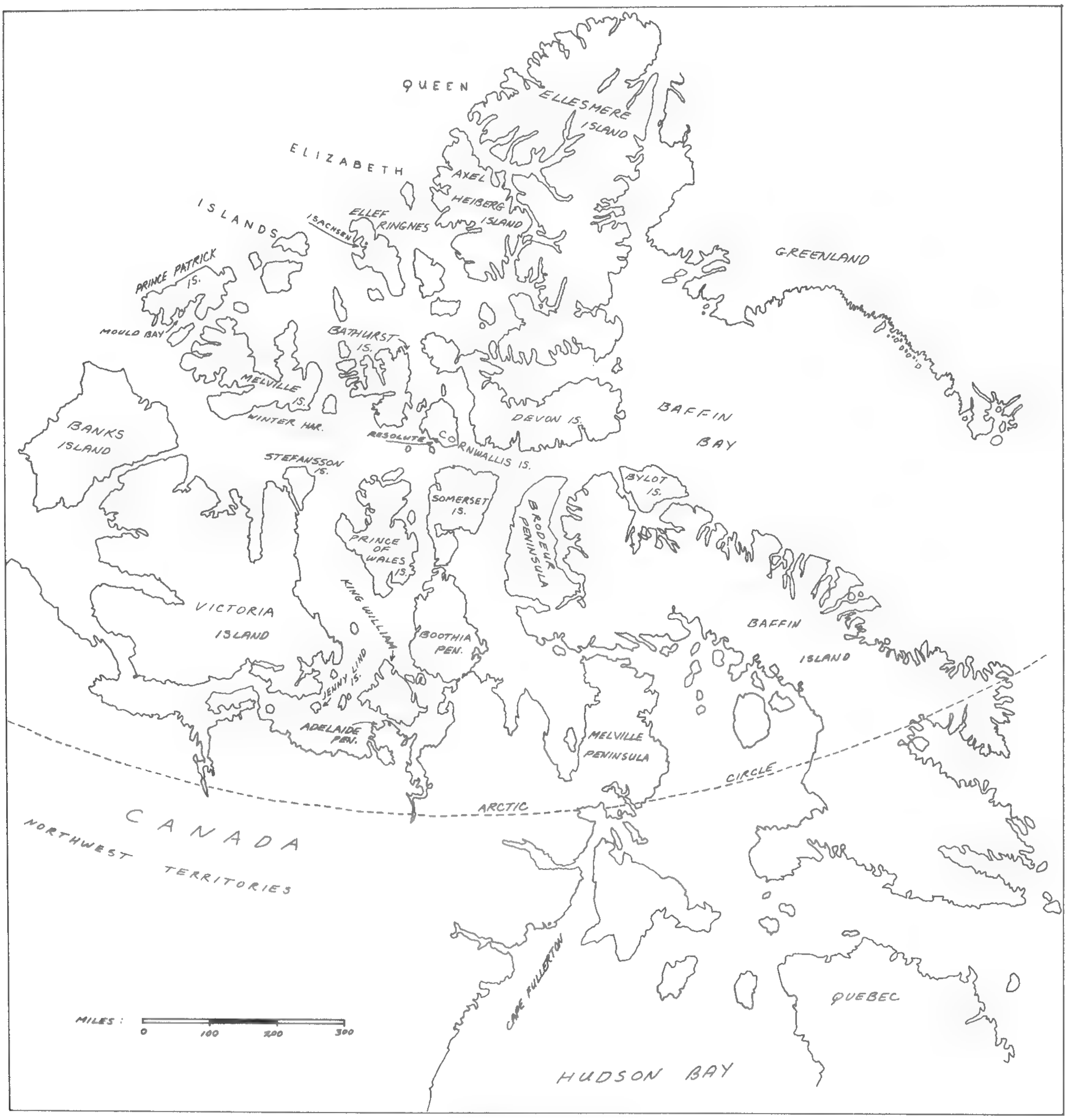


Figure 1. Map of Northwest Territories showing Bathurst Island, the site of this study.

bation is a problem we failed to solve. Young birds were simply banded: 19 of known age on the left leg exclusively; 15 of uncertain age on the right leg.

In 1969, the only birds banded were four siblings at a nest west of camp by Taylor. Gray, Taylor, and F. Pierre Lamothe continued general observations on Sanderlings after I left Bathurst Island on 29 June.

Sexing live Sanderlings is a major problem. The males of paired birds generally are considerably brighter than females with the rusty color of the head, neck, and upper pectoral regions more intense and extensive as a rule, a condition not so obvious in dry skins. Most paired birds showed this dimorphism clearly when side by side, but we noted exceptions — some bright females and some very gray males. When seen singly we had difficulty in determining the sex of these odd birds and had to rely on behavioral characteristics and certain call notes, which even now we do not fully understand. Although we were fairly certain of the sex of the incubating individuals at most of the nests that we watched for some time, we were not always dead certain. We claim no fool-proof method for determining the sex of Sanderlings in the field but merely call attention to the problem.

Few authors attempt to describe differences in the breeding plumage of the sexes, either ignoring the problem or describing the sexes as similar. Palmer's description (1967) is about as good as there is. The female differs from the male in having paler rusty on the head and anterior underparts; some have white throats and hardly any rusty on breast. We noted that some fairly

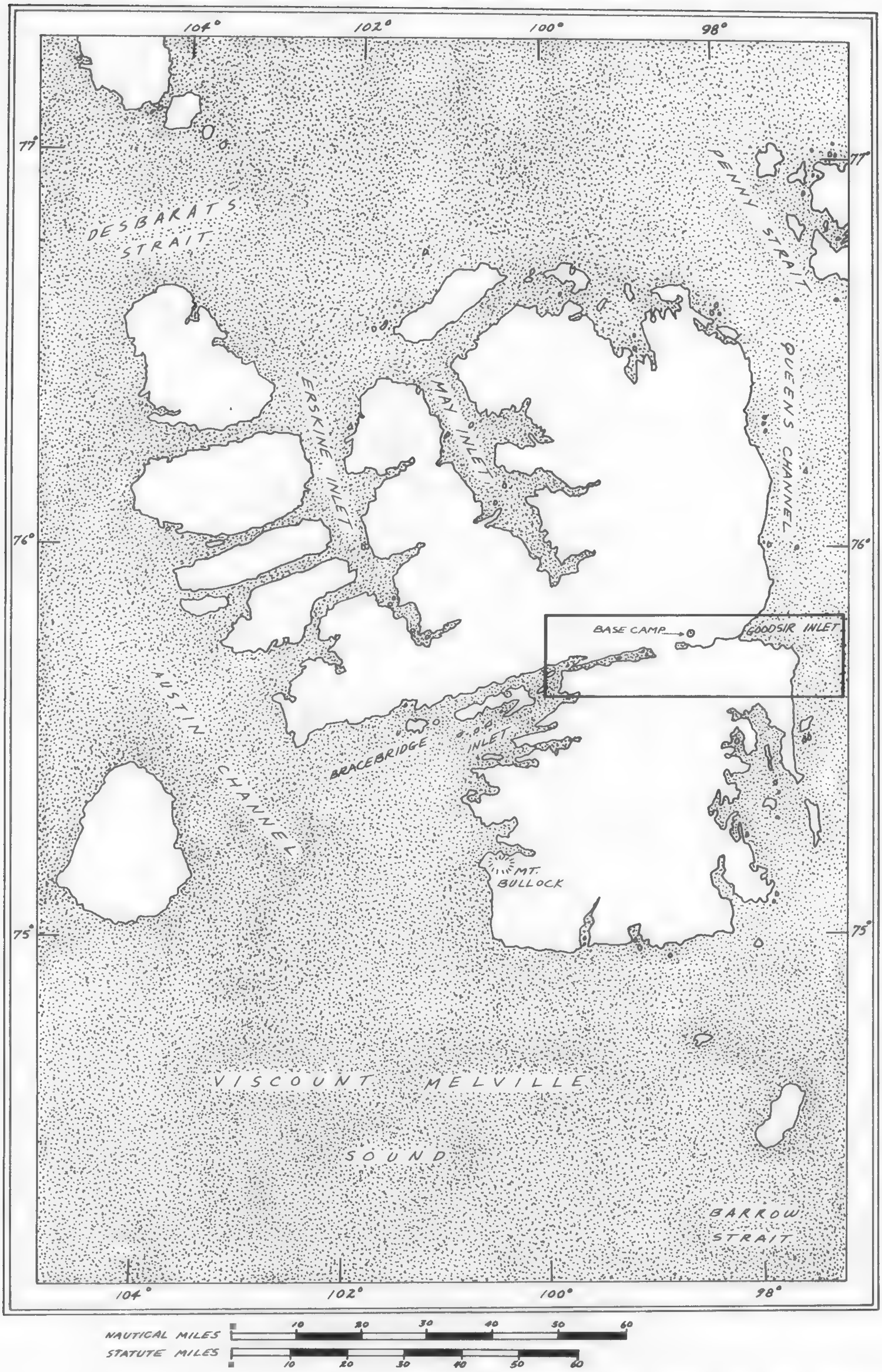


Figure 2. Bathurst Island, showing the location of the base camp. The rectangular area is shown in greater detail in Figure 3.

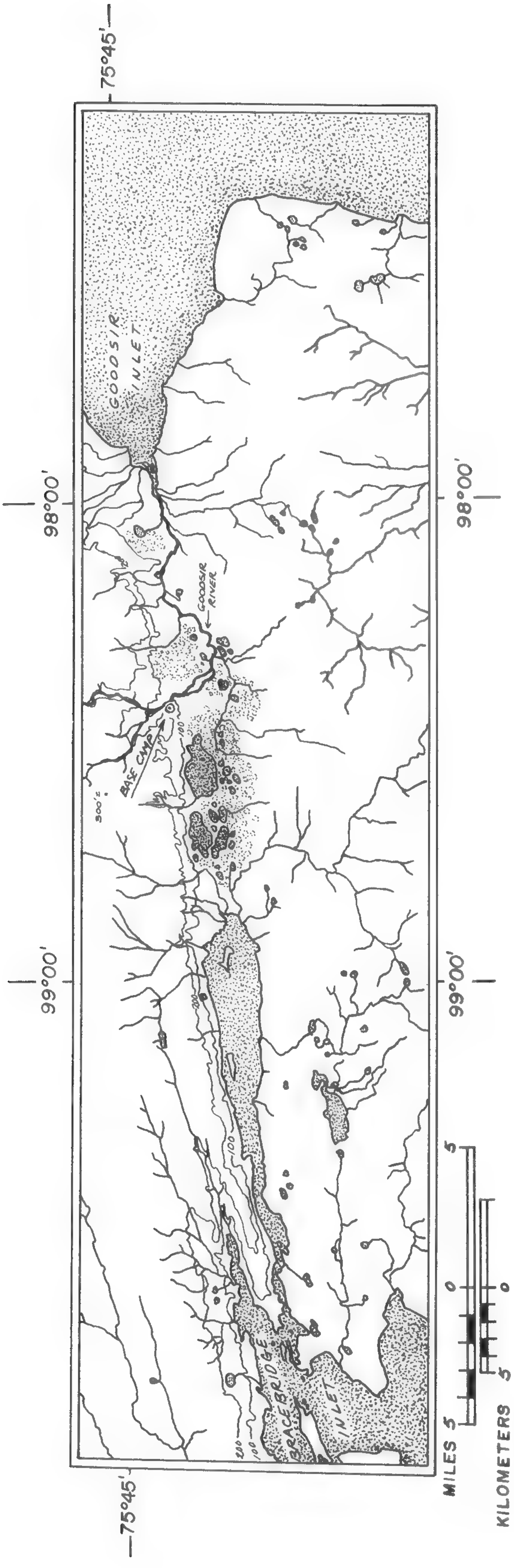


Figure 3. The base camp region (rectangular area in Figure 2) shown in greater detail. The area between the two inlets is dotted with valleys, lakes, and marshy ponds.

bright males also have whitish throats. Interestingly enough, Pedersen (1942) described the summer bird as having "two distinctly different appearances — one red-brown, the other one grey." Referring to the color of the neck and back, he stated that both forms "occur in equal numbers everywhere in its area of distribution." He did not say that the dimorphism was sexual, nor did he imply it.

There is a slight sexual dimorphism in size. Females average larger, a condition especially noticeable in wing measurements. According to Manning *et al.* (1956), bills of females average longer. Because of an apparent overlap in bill lengths, one can separate probably only 80 to 90 per cent of the birds on this character alone.

Breeding Distribution in Canada

The Sanderling, a monotypic species, breeds principally in the high Arctic. Although it has a circumarctic distribution, it does not breed continuously around the polar region. Its better known breeding grounds include northern Greenland (Hall and Peary Lands), northeast Greenland south to Scoresby Sound, and Spitsbergen. The extent of its breeding in the Soviet Union is little known, though Gladkov (Bannerman, 1960) reported nesting grounds on the Taimyr Peninsula, Svernaya Zemlya, New Siberian Islands, and at the mouth of the Lena River. It is a rare breeder along the arctic coast of Alaska, and, despite the abundance of the species and the numerous expeditions into the arctic islands, its breeding range in Canada is ill defined.

Roderick R. MacFarlane discovered the first authentic nest of the Sanderling on the mainland of Canada, in the Franklin Bay area east of Fort Anderson, on 29 June 1863, although a Sanderling egg, purporting to be a Purple Sandpiper's, apparently had been collected by Sabine as early as 1823. MacFarlane (1908) considered the Sanderling a rare breeder in the Franklin Bay area where a nesting has not since been reported.

The status of the Sanderling elsewhere along the mainland coast is equally uncertain. Low (1906) reported "Skins and eggs from Fullerton" (Cape Fullerton, northwest Hudson Bay), but the record is vague. On Southampton Island nearby, the species probably breeds at least sparingly — a belief based on reports by Eskimos and juvenile specimens with much natal down (Sutton, 1932). Presumably, Sanderlings breed at least sparingly north and west of Southampton on Melville and Boothia Peninsulas. However, Macpherson and Manning (1959) did not even record the species as a rare breeder on Adelaide Peninsula.

The great numbers of Sanderlings that come south from the Canadian breeding grounds almost certainly originate on the arctic islands, but even there they are not uniformly distributed. Sanderlings appear to be practically absent from huge Baffin Island though no one has explored Brodeur Peninsula for them especially. Records for Bylot Island northeast of there are scarce: Tuck and Lemieux (1959) believed that at least "two pairs" bred on the northwest coast where a "female with a well-developed brood patch" was collected on 20 July 1957 and Drury (1961) reported, for the south coast, only one bird performing a "distraction display."

Farther west, on the southern part of King William Island, the species very likely breeds at least sparingly, as it does on Jenny Lind Island and probably in southern Victoria Island (Parmelee *et al.*, 1967). A major breeding ground is Prince of Wales Island where a large population summered in 1958 (Manning and Macpherson, 1961). Probably Sanderlings breed commonly elsewhere in the central islands (northern King William, Somerset, northern Victoria, Stefansson), but we have no direct evidence. Banks Island in the far western part of the archipelago is certainly a major breeding ground (Manning *et al.*, 1956).

In the northernmost islands of the archipelago, the Queen Elizabeth Islands, the species is decidedly scarce in the mountainous eastern section. For Ellesmere Island, Sanderling records, including some of nests, date back to 1878, but none suggests that the species ever approaches even modest densities. Sanderlings appear to be equally uncommon on rugged Axel Heiberg Island. According to David J. T. Hussell (pers. commun.), they breed sparingly in northeastern Devon Island.

In the extreme northwest, on Prince Patrick Island, Sanderlings bred commonly at Mould Bay in 1949 and only four were observed in 1952 (MacDonald, 1954). Although data on the yearly fluctuations in numbers of nesting Sanderlings are scarce, doubtless these fluctuations occur.

A probable major breeding ground east of Prince Patrick Island is Melville Island where Sanderlings were common at Winter Harbour years ago (Hennessey, 1910), but that island remains mostly unexplored ornithologically.

The Sanderling's status on Bathurst Island heretofore was almost unknown. Harington (1961) recorded the species twice on the tundra between Goodsir and Bracebridge Inlets in 1961, one bird on 29 June and two on 1 July. However, we believe that this area, and probably the vast lake areas in southern parts of the island, may be an excellent breeding ground for Sanderlings in some years.

The barren stretches of northern Bathurst appear to be poorer nesting grounds, and some of the islands northward even less suitable, if the Isachsen area of Ellef Ringnes Island is any indication; MacDonald (1959) did not record the species there at all. The density of Sanderlings may be low east of Bathurst on Cornwallis Island as well; Urban (1957) failed to record one there though I and others have since seen a few at Resolute Bay. Grinnell Peninsula in western Devon Island conceivably is more favorable.

Since MacFarlane's discovery in 1863, there have been few nests reported from arctic Canada. Feilden (1877) reported a nest with two eggs at 82 N Lat. on the north coast of Ellesmere Island on 24 June 1876; Parmelee and MacDonald (1960), one with four eggs, two pipped, at 80 N Lat. near Slidre Fiord in west-central Ellesmere Island on 12 July 1955; Parmelee *et al.* (1967), one with four fresh eggs at 68 N Lat. on Jenny Lind Island on 24 June 1966. With observations of broods almost as scarce, it is no wonder that little is known of the Sanderling's breeding.

Breeding Density

We have few estimates of the population densities of Sanderlings on the nesting grounds. Manning *et al.* (1956), by converting the number of Sanderlings recorded per hour in a given area to an estimated standard number per square mile (multiplier technique), concluded that an adult population of 65,000 birds summered on Banks Island in 1952. Although pairs nested throughout the 24,600-square-mile area, the principal nesting ground was on the western side. The same authors thought that only the Semipalmated Sandpiper (*Ereunetes pusillus*), with an estimated population of 70,000 birds, was more abundant than the Sanderling. They found the other sandpiper species much less abundant: White-rumped Sandpiper (*Erolia fuscicollis*) and Baird's Sandpiper (*Erolia bairdii*), 25,000 birds each; Pectoral Sandpiper (*Erolia melanotos*), 14,000 birds; and Buff-breasted Sandpiper (*Tryngites subruficollis*), 2,000 birds. They gave no figures for the largest number of Sanderlings per square mile for any one area.

On Prince of Wales Island and its small adjacent islands, 12,500 square miles, Manning and Macpherson (1961) estimated the Sanderling population at the beginning of the 1958 nesting season to be 70,000 birds — a population more than twice as dense as that of Banks Island in 1952. Numbers of Sanderlings varied from place to place, ranging in density from 3.5 to 35.0 birds per square mile, and was greatest in the Inner Browne Bay area on the east side of the island, but low in the "rather barren, lakeless, inland country."

Manning and Macpherson considered the Sanderling the most abundant sandpiper on Prince of Wales Island, placing Baird's Sandpiper second (40,000 birds) and the White-rumped Sandpiper third (15,000 birds). This is the only reference putting the Sanderling first in order of abundance on any Canadian breeding ground.

In 1968 the Sanderling was by far the most abundant sandpiper in our study area on Bathurst Island, the Knot (*Calidris canutus*) being only a third to half as abundant and other sandpipers much less. Nevertheless, we hesitate to list the Sanderling as a truly abundant species on Bathurst Island that year, because the pairs were thinly scattered — less so than other shorebirds, however. In 1969 the Sanderling was decidedly uncommon, even less common than Knots.

At Bathurst we visited various areas in the broad, lake-dotted valley between Goodsir and Bracebridge Inlets and concentrated on Sanderlings in two. The first area was a strip of ridges and marsh, roughly a mile wide, that extended six miles west from camp toward Bracebridge Inlet. For the most part the ridges lay in straight lines paralleling the marsh that formed the north shores of the two largest lakes in the valley. Within this six-square-mile area we found five Sanderling nests, five broods (unmarked) of small downy young, and two broods of larger young which may or may not have hatched there. Ten pairs, and possibly 12 or more, bred in this area in 1968.

Sanderlings were scattered all along the six-mile strip during the arrival period and for some days following. With the onset of nesting, some of the pairs concentrated in certain areas. Four of the five nests were within an area five to six miles west of camp; three of the four nests were within a half mile of one another; and two were only 352 paces apart. In another concentration, just west of camp, at least four pairs (one nest, three broods) resided in a one-square-mile area.

The second study area was roughly four square miles of variable terrain — ridges, alluvial plains, marshy ponds — extending north, east, and southeast of camp. Here we found five nests and two broods of fairly old young. These too were concentrated with three nests within a one-square-mile area, and two only 520 paces apart.

The three to four pairs per square mile was the greatest concentration of nesting Sanderlings recorded by us on Bathurst Island. Considering that predators probably destroyed the eggs of some pairs before we found them, that we certainly did not find every brood, and that the late thaw may have kept some pairs from nesting, I believe that the resident population probably did not exceed six to eight pairs per square mile in the choicest areas on the Bathurst breeding ground in 1968. The density in 1969 was much less, perhaps only one to two pairs per square mile.

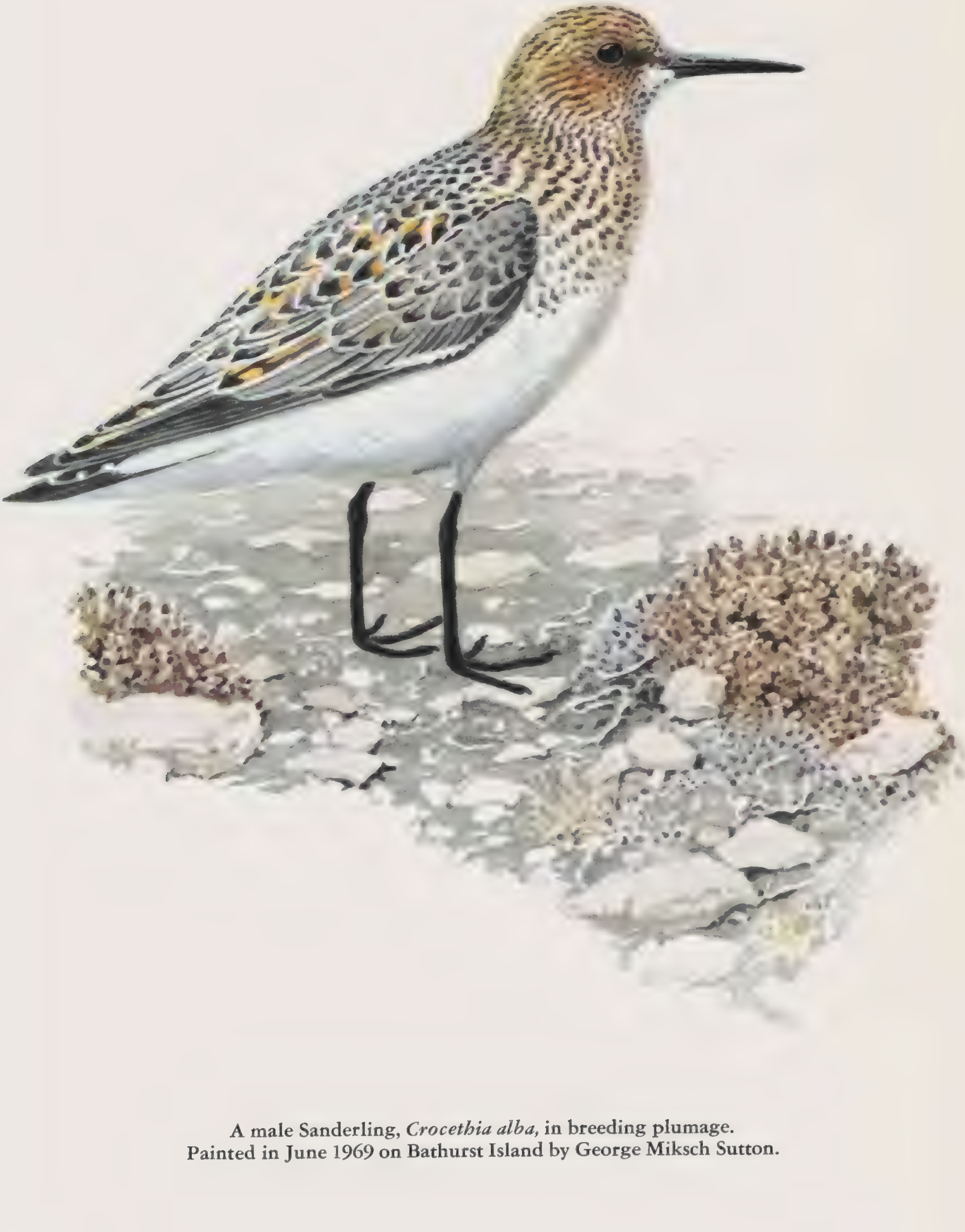
Although Manning and Macpherson (1961) did not locate nests or broods, they did estimate the adult population on Prince of Wales Island at the onset of nesting. If their figures are taken at face value, it appears that upwards of 17 pairs of Sanderlings may occupy a one-mile-square nesting ground, a reasonable figure considering the proximity of some nests on Bathurst Island. Manniche (1910) gave no data on population densities for the Greenland breeding ground, but one can surmise that Sanderlings are numerous there at times. Although he found only 11 nests during 1907–1908, he observed some 50 broods – itself highly indicative of a dense population. Such a breeding ground has not yet been found in Canada, unless it is on Prince of Wales Island.

Arrival on Breeding Ground

Arrival dates for the Sanderling on the Canadian breeding ground are scarce, practically none for the eastern Arctic, and little more for the western Arctic. Hennessey (1910) reported that Sanderlings arrived at Winter Harbour, Melville Island, on 1 June 1909 but gave no details. On Banks Island (Manning *et al.*, 1956) Sanderlings arrived at De Salis Bay in 1952 no earlier than 8 June. In 1953 the same authors saw a flock of 24 birds at Cape Kellett on 30 May and 100 birds during a four-hour walk there the following day. Presumably both sexes were present. Macpherson and Manning (1959) noted migrating Sanderlings during 14–16 June 1957 on Adelaide Peninsula where the species is not known to breed. Parmelee *et al.* (1967) saw no migrating Sanderlings in spring along the southeastern coast of Victoria Island but witnessed the arrival of the birds on Jenny Lind Island nearby. There, on 7 June 1966, they saw what appeared to be the first Sanderlings–a flock of 13 of both sexes–at a marshy pond two miles inland and on the following days noted widely scattered pairs, invariably a bright male and a dull female.

The arrival is better known for Greenland. According to Salomonsen (1950–1951), the spring migration takes place extremely rapidly, there being no spring records for southeast Greenland and none south of Disko Bay on the west coast. The birds arrive on the breeding grounds in late May and early June. At first the Sanderlings move about in "flocks of 8–12 individuals, frequenting the sea-shore and the few spots free of snow." After a "couple of days they are paired" and move inland to the breeding places. Pedersen (1930) recorded the arrival near Scoresby Sound, respectively, on 26 May 1928 and 2 June 1929; the birds immediately proceeded to the interior of the fiord where during the first days they went about in groups; after 8 June they "paired off" and two days later left the coast for the inland breeding ground. Manniche (1910) made the point that the Sanderlings arrived at Stormkap "singly or in couples," respectively, on 2 June 1907 and 28 May 1908, though he believed that "pairing began towards the middle of June." He further stated that the Sanderlings at Stormkap in the first days after their arrival resorted to snow free areas in the marshes and on the surrounding stony plains in company with other waders and large flocks of Snow Buntings. According to his experience, the "old birds would never resort to the salt water shore."

The first Sanderlings, seen on Bathurst Island in 1968, were well inland. Two birds of undetermined sex flew by me some five miles east of the head of Bracebridge Inlet on 3 June. The same day Hampson watched a mixed flock



A male Sanderling, *Crocethia alba,* in breeding plumage.
Painted in June 1969 on Bathurst Island by George Miksch Sutton.

of eight birds, four bright and four pale, that had alighted near camp. We saw none the following day, but by 5 June single males were displaying in widely separated places, and the male and female of one pair that flew and fed together behaved as if they were mated. We saw no Sanderlings immediately along the ice-locked shores of Bracebridge Inlet where there was little melt water on 5 June.

The Sanderlings continued to arrive inland. A mixed flock of 10 birds flew along a ridge three miles west of camp on 7 June. We saw the last flock, seven birds of both sexes, feeding on muddy ground, where the thaw was most evident, a mile north of camp on 9 June. No other species accompanied these flocks although the Sanderlings in the flocks, both single and paired birds, shared the feeding areas with other species. Pairs increased daily after 5 June until, by 11 June, the Sanderling was the most abundant wader on the tundra between Goodsir and Bracebridge Inlets—a distinction it held for the remainder of the season.

Paired birds were inseparable. When one of the pair flew, the other quickly followed. On the ground the bright male walked with a jerky gait and chattered loudly on occasion while the female, usually much duller and always somewhat agitated, followed and regularly uttered a sharp, one-syllable note in our presence.

Because of the considerable individual variation in the plumage of these birds, we were reasonably certain that we saw the same pairs time and again in special areas where they walked about and fed. The female of the pair that frequented our camp, for example, was excessively pale. Although certain pairs left their special loafing and feeding areas for long periods, they nevertheless returned often enough to hold our attention. So attached were they to the special slopes and ridge tops that we spent much time in those places searching for nests. Not until later did we discover that these birds nest in different areas and usually mate in still others (see Precopulatory Scrapes below).

In 1969, Sanderlings arrived on Bathurst Island somewhat later. The first that we recorded inland flew along the frozen valley northeast of camp on 6 June, and a mixed flock of six birds visited camp on 8 June. Except for one pale individual on a ridge two miles west of camp on 10 June, we did not see the species anywhere during 9–11 June. The bulk of the Sanderlings appeared between 12–15 June when we saw singles, pairs, and a few mixed flocks of five to 10 birds each. Thereafter, we noted only thinly scattered singles, pairs, and triplets.

Both sexes arrive together on the inland breeding ground in small flocks of probably from two to 13 or more birds. Some of these birds seem to be paired on arrival although we have no proof of this. It also appears that most Sanderlings go about in pairs soon after the flocks break up. Single, unmated Sanderlings, seemingly a small minority, occur both early and late in the season. Whether these birds arrive alone is uncertain. Many of these points need further study.

Territory

The territory of the Sanderling is basically a plot of level or sloping, wet or dry, ground over which the male performs flight displays in advertising for a mate, and which, until he pairs with a female, he defends vigorously against other males of his kind. We did not determine the precise limits of any one territory. It seemed to include an area approximately equal to that covered by the male when performing flight displays—an area with a radius of roughly 200 yards. The territories were so widely scattered on the Bathurst Island breeding ground that we were never aware of two or more of them close enough to be a source of constant fighting, though conceivably this does happen.

The problem is further complicated by unmated males which appear to be relatively few in number, but which do most, if not all, of the performing and defending. These males do not defend their territories at all times. They appear on them sporadically for indefinite periods. Several different males may use certain favored areas, each in turn, no two displaying or defending at once. Such was the case a quarter-mile from our camp on a well-defined slope frequented by both Sanderlings and members of our expedition. In 1968, a very bright male displayed there as early as 13 June; another exceedingly dull male displayed there on 9 July, our latest date for flight-displaying though we heard flight-singing until 13 July. At least four different males performed on the slope at various times that year.

We may question the size and use of the territory, but not its defense. A male, when present, defends his chosen ground to the limit—a fact appreciated by Manniche (1910) who stated that the male also defended it against other species. We noted defense against Sanderlings only. The defending male quickly flew to a strange Sanderling entering his ground. If it were a lone male, he chased it hard. If it were a lone female, he courted. The male also investigated all pairs, and the confrontation that followed often ended in a swift flight chase by the trio. Sometimes both members of a mated pair turned on the single male and attacked it viciously with body-to-body contact.

The conspicuous flight chases by three or four birds is a phenomenon common not only to Sanderlings but to many other shorebirds as well. Presumably both sexes take part but this is not well documented. Our observations on the Sanderlings, the sexes of which can usually be separated during breeding time, may shed some light. Such chases often started with a confrontation between a single defending male and a mated pair. MacDonald's observation in 1968 is of special interest: At 00:05 hours on 18 June a performing male flew down and landed within five feet of a mated pair. The paired male immediately raised his scapulars, lowered his head, and rushed at the single male which erected his feathers and charged, but then turned and ran. The female, meanwhile, left the ground and flew close to the single male which leaped into the air after her. The mated male followed him and the trio flew off in a typical erratic flight. Eventually they broke up while flying. The female flew down to the ground, her mate glided in behind on V-set wings, and the defending male continued flight-displaying. He was still displaying when MacDonald left at 03:30.

Paired birds walking about in undefended areas usually ignored one another. Occasionally a confrontation between pairs terminated in a flight chase when one of the females jumped out in front of the others and flew off. Invariably the males and sometimes the remaining female followed her. So it appears that the female may initiate a flight chase which may or may not concern territorial defense.

Flight Display

In 1968, we first noted Sanderling flight displays less than half a mile from the head of Bracebridge Inlet on 5 June – within two days of the species' arrival and one of few pleasantly mild days that month. Flying up from wettish spots and moving low for short distances above the gentle snowy slopes, two widely separated males rose on rapidly vibrating wings and sang lustily. Dropping down to exposed turf, they soon performed again. Another male flew and sang above low-lying ridges, partly free of snow, three miles east of the inlet, and we were certain that courting activities would soon be common in many places.

The weather turned for the worse on days following. Flight-displaying, like the thaw, never did rush forward on a broad front in the Goodsir-Bracebridge area. Although Sanderlings were more persistent in displaying during inclement weather than other shorebirds, including Knots, their display activities were highly sporadic and usually brief. Sanderlings displayed vigorously during calms or low winds even though the air was frigid and the ground beneath them mostly snow covered. High winds seemed to inhibit their displaying more than any other physical factor yet were not the only factor influencing flight display.

From the beginning the males did not perform flight displays before females. Almost invariably a displaying male flew or hovered above an area where we could not find a female. According to Manniche (1910), flight-displaying (called "pairing display" by him) can take place without the presence of a female. This indicates that flight display of the Sanderling, like its territory, functions primarily in advertising for a mate. If this is true, the display probably falls off sharply or ceases with the establishment of a pair-bond. Although we observed many pairs on the ground for long periods, we never saw a male suddenly leave his mate and perform. Since most pair-bonds form early, only unmated males are left to perform and they may at times be so scarce, especially during those years when the population is low, that one may not notice any flight-displaying.

Of the relatively few Sanderlings we saw on the Jenny Lind Island breeding ground in 1966, all formed pair-bonds before or soon after arrival. It may be significant that we saw no flight display there that year, and that we recorded flight-displaying only twice, 19 and 21 June, on Bathurst Island in 1969 when the population was low.

Manniche (1910) briefly described the flight display of the Sanderling, stating that the male uttered a snarling or slight neighing sound, mounted to a height of some two meters from the ground on strongly vibrating wings and continued his flight for a short distance at this height, most frequently in a straight line but sometimes in small circles.

We noted the display a number of times on Bathurst Island in 1968. In flight, the forward part of the male's body is more or less parallel to the ground, the tail is level with the body, or down turned, and usually somewhat

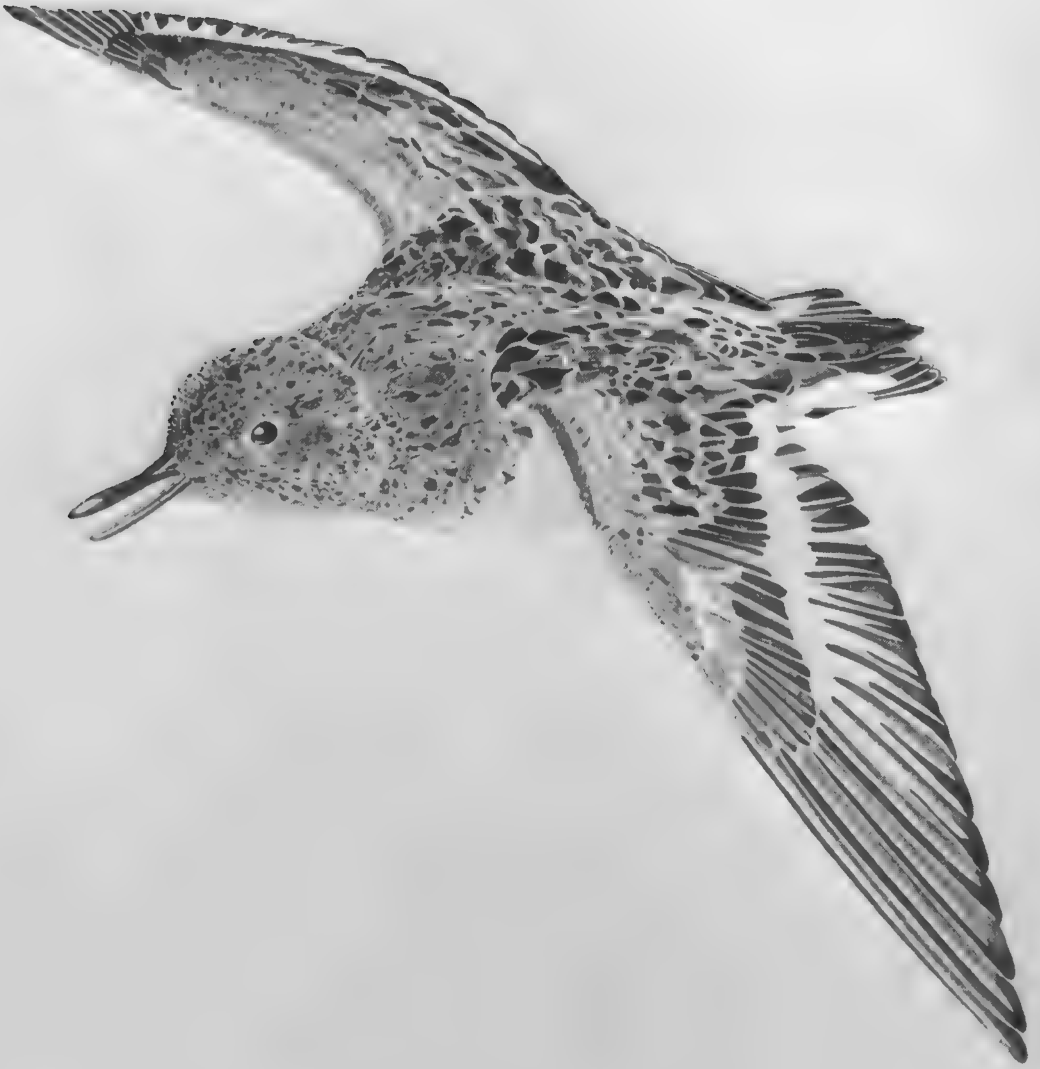


Figure 4. While performing its flight-display, the male Sanderling moves its wings up and down through a 45-degree arc at such great speed that they literally vibrate. The rapid wing-beats are not continuous but in bursts, and each burst is followed at irregular intervals by a brief pause during which the wings remain perfectly immobile. The white of the wing, which is still clearly visible during rapid wing-beats, is shown in detail in this drawing which I made directly from the spread wing of a mounted specimen.

spread; and the head is drawn back presenting at times a hunched appearance—also typical of the displaying bird on the ground. The head and bill are pointed straight ahead or turned down slightly; both move frequently from side to side as the bird surveys the ground below. The wings, held straight out from the sides of the body, move up and down, through a 45-degree arc, at such great speed that they literally vibrate, although the prominent white wing-bars are still clearly visible (Figure 4). The rapid wing-beats are not continuous but in bursts, and each burst is followed at irregular intervals by a brief pause during which the wings remain perfectly immobile, fully extended, and parallel to the ground. The rapid wing-beats through the narrow arc, followed by the brief pauses, produce a most peculiar flight.

The ascent from the ground may be rapid or slow, as may be the forward flight above ground and the descent. The bird descends either abruptly or slowly in a long arc, sometimes with wings extended and held far out, resulting in a glide. On occasion the bird descends to a foot or two above ground and flies for many yards before touching down. Many times a bird about to land suddenly picks up momentum and continues displaying. It may repeat this performance several times before landing.

Manniche (1910) did not mention hovering by displaying Sanderlings, and I find no reference to it. It is true that the male often performs a complete flight-song without hovering; in other words, the bird moves forward continuously. But frequently a displaying male stops in midair and hovers in one spot, during which a series of rapid wing-beats are followed by brief pauses, as when the bird moves forward. The hovering at times is very conspicuous, and we once timed a hover that lasted fully two minutes. On the other hand, the entire flight display, from take-off to touch-down, may take as little as 30 seconds or even less.

The height of the display flights is said to be very low—only "two meters" (Manniche, 1910), only "as much as 15 ft." (Witherby *et al.,* 1940), and only "2–3 metres" (Salomonsen, 1950–1951). We saw Sanderling males performing commonly from 15 to 30 feet above ground and occasionally 60 feet or more. Even these high flights, however, do not approach the high flights of certain shorebirds. Compared to the Knot, Stilt Sandpiper (*Micropalama himantopus*), and Hudsonian Godwit (*Limosa haemastica*), the Sanderling is essentially a low-altitude performer.

The flight display of the Sanderling has been described simply as one that covers a "short distance," meaning a small area of ground. Once again, compared with those of the Knot, Stilt Sandpiper, and Hudsonian Godwit, the statement is valid. We measured the distance from point of take-off to point of touch-down several times and estimated the distance a good number of times, finding that most displays fell within a radius of 200 yards. Occasionally males covered a much greater distance, and sometimes flew out of sight. Displaying birds flew in a "straight line" or "small circles," as described by Manniche (1910); also, erratically with no clear-cut direction at times.

The song of the flight display is highly complex, so difficult to describe in terms of phonetics that I hesitate to try lest I add to the confusion of the various renditions given it by others. However, I can say that the song was loud and distinct, given by performing males above ground, and occasionally by performing males on the ground immediately preceding flight display. To all of us the notes seemed so frog-like that I refer to it as the frog song. Like the rapid wing-beats during display, the song was delivered in bursts, though we could not be sure that the wing-beat and song were synchronized. The frog song was frequently, yet not invariably, followed by chattering notes during the descent immediately before the flight terminated. The chattering notes, equally difficult to describe, were of a familiar type given by non-performing birds. We taped both calls under adverse conditions.

We believe that female Sanderlings performed flight displays, heretofore unreported in the literature, at least a few times on the Bathurst breeding ground in 1968, but we did not collect a displaying female for positive identification. However, I saw such a display on 18 June the following year. The pale bird of a pair, that I had been watching for over an hour, suddenly left the ground on rapidly vibrating wings, ascended to a height of 30 feet, descended 10 feet, ascended again, and finally glided down to a muddy slope where it was immediately joined by the much brighter mate which gave every indication of being a male. The flight was like that of a male, except that I heard no vocalizations of any sort, and the bird did not hover. The peculiar mating behavior (described below), following the flight, indicated that the pale bird was almost certainly a female and not merely a pale male involved in the phenomenon of reversed copulation. What the adaptive function of such a display could be is puzzling, unless it is one of a number of devices employed by the female in strengthening the pair-bond which in Sanderlings appears to be weak. Possibly the female display reduces hostility between the sexes, or simply advertises the nesting ground.

Ground Display

Manniche (1910) evidently saw pairing take place on the breeding ground in northeast Greenland. He described the male as frequently sitting on "... top of a solitary large stone, his dorsal feathers blown out, his tail spread and his wings half let down, producing his curious subdued pairing tones." He further stated that the male ". . . soon returns to the female, which always keeps mute, and then he tries by slow affected, almost creeping movements to induce her to pairing, until at last the act of pairing takes place; when effected both birds rush away in rapid flight to return soon after to the nesting place." Manniche's meaning of the term "pairing" is not clear. Salomonsen (1950–1951) interpreted the findings of Manniche and others to mean that, following flight-displaying, the male displayed to the female either from a protruding boulder or rock or by running on the ground, and that copulation followed. These authors give the impression that copulation, not merely the establishment of the pair-bond, follows displaying immediately. Whether display by the male alone initiates copulation is questionable. In observing precopulatory behavior (see below) many times, we concluded that females, not males, initiate successful copulation.

We were not certain that any of the ground displays (never on a rock), observed on Bathurst Island, were steps leading to establishment of a pair-bond. Some appeared to be. The first occurred on 7 June when a bright male ran with a dull female near the top of a wind-swept ridge. With head drawn far back against shoulders, bill straight ahead, feathers erected, tail slightly depressed, and wings drooping with primaries partly spread, he closely followed the female until the run terminated in a flight.

Some ground displays were dramatic. On 26 June a single bright male with his head so withdrawn and feathers so puffed out that he appeared ludicrous ran up a muddy slope to a pale female. Uttering notes almost inaudible in the wind he extended both of his wings fully and arched them down near the tips, causing the somewhat spread primaries to drag on the mud and wet turf. He spread his tail and turned it downward. Viewed from the back, the white of the tail was nearly continuous with the white of the wing-bars, and we wondered whether this bold display of white ever functions as a releaser. In this case, it did not.

Because we never witnessed copulation following displays of this type, we felt that the birds were not truly paired. Nearly all copulatory activity among the Sanderlings occurred in areas quite apart from the areas where the birds nested though single males occasionally performed flight displays over or near such areas. Invariably, the female initiated copulation by displaying in special nest scrapes that we called precopulatory scrapes.

Precopulatory Scrapes

Although a few Bathurst Island Sanderlings may have had eggs as early as 16 June in 1968, the pairs we watched did not lay before 20 June. That day, on a flat stony terrace just up from a slushy stream bed, a pale Sanderling ran toward us scolding. Flying off once, it quickly returned and scolded again. We backed off and watched this bird, which we believed to be a female, but it did not go to a nest.

The following day a bright male was with a pale female, likely the one seen earlier, in precisely the same place. With head withdrawn and feathers fluffed out, he immediately voiced protest. Then both birds put up such a fuss as to make us feel certain that one of several neatly lined scrapes found there had to be the nest. The pair especially favored one scrape, a rather deep cup freshly lined with dry willow leaves and lichens and surrounded by *Dryas*. We called it Nest 1 and erected a blind nearby.

On 22 June at 02:30 hours, Hampson and I watched the pale female settle in Nest 1 with head low and tail almost vertical. She squirmed a little, and the male which had been standing close by ran and thrust his bill down beside her and several times removed bits of lining from the scrape. Then he stood on her back, stepped off, and deliberately eased her out of the scrape with his bill and forehead thrust beneath her belly. Both then ran off side by side with bodies pressed together and rubbing vigorously. Having run some 10 feet, the male lowered his head and pressed his bill forcibly against the breast of the female, immediately stopping her. She stood still and copulation followed.

We thought his mating procedure most unusual and wondered if it was typical. Later on 24 June, at 04:30, we saw a pale female settle low in a scrape about a hundred paces from Nest 1. Her head was hidden from view, but not so her posterior which was elevated high above the scrape and surrounding stones. As before, the male ran up and deliberately eased her out with bill and forehead, though he did not pick at the lining of the scrape and stand on her back this time. Both ran for 10 feet, rubbing sides as they went, the male seemingly rubbing the hardest and running about a half step behind. Once again he stopped her by pressing his lowered bill against her breast. Immediately the female stood still and the male mounted. Later, when the female investigated other scrapes, squatting in one of them, the male, some distance away, did not respond. Eventually they flew off together and disappeared over low-lying hills.

After these two instances we saw remarkably similar behavior among other Sanderling pairs. The sequence of the female squatting in the scrape with rear elevated, the male easing her out with his bill and forehead, the side-to-side-rubbing-run, and the breast-pressing, followed by copulation, all appeared to be basically typical and similar with some variation. Taylor made additional observations at 07:30 on 24 June: When a male first approached a squatting female, he walked around the scrape six times with his shoulders and sides brushing hers; the male positioned himself a full step ahead of the female near the end of the side-to-side-rubbing-run, and by the time the female had stopped running, the male was facing her nearly head-on with forehead as well as bill pressed hard against her breast.

At least four widely scattered pairs used scrapes on the stony stream terraces north of camp for mating purposes. Other pairs used similar precopulatory scrapes on the ridges west of camp. All of the scrapes, including Nest 1, were eggless. We continued to watch them although we soon learned that the Sanderlings using them were nesting elsewhere, seemingly a long way off in some cases. However, we did see precopulatory scrapes and copulatory activity sparingly in a nesting area both years.

Upon closer inspection, the precopulatory scrapes appeared to be old nests, possibly of other species and perhaps used later by Sanderlings. Compared to genuine Sanderling nests, they were often larger and invariably deeper, neater hollows. The active movements of the Sanderling smoothed the scrape and gave it the unmistakable appearance of freshness.

We studied Sanderling precopulatory behavior with renewed interest on the Bathurst breeding ground in 1969, but noted only one behavior that we had not observed the previous year. On several occasions I heard a female, positioned carefully in a scrape, utter low buzzing notes—not unlike the sound of a typewriter carriage in motion – while awaiting the male. The buzzing notes appeared to attract the male and in conjunction with body posture may have functioned as enticing notes. Unfortunately, we did not record them.

That Sanderlings use old scrapes during precopulatory activity there can be no doubt. In 1969 a pair of Sanderlings used a well-defined scrape that I had marked with rocks in 1968. To our knowledge no Sanderlings had used this particular scrape the first year. Conceivably, Sanderlings make precopulatory scrapes when none exist. The Bathurst breeding ground is literally covered with scrapes that probably last for years under desert conditions of the high Arctic. Pedersen (1942) noted that the Sanderlings in Greenland used empty scrapes which he called "playing nests," stating that they were a "self-dug hollow lined with dry *Dryas* and *Salix* leaves." He did not know their function, but speculated that the "birds wanted to throw off possible enemies with these nests by sitting on the empty nest as if brooding and flying away abruptly when the intruder had approached the nest to a distance of a few steps."

Copulation

No one has described copulation in the Sanderling. Manniche (1910) stated that the "act of pairing" was the "completing act" that followed flight and ground displays. Presumably his "act of pairing" meant copulation.

Salomonsen (1950–1951) arrived at the same conclusion. Unfortunately, Manniche was vague on this point and made no attempt to describe the act in detail; conceivably, he never witnessed it.

We watched copulation in the Bathurst Island Sanderlings at least a dozen times during 22–26 June in 1968, and again during 18–25 June in 1969. Invariably, it occurred after a female squatted in a precopulatory scrape or hollow and, usually, after the birds had completed the side-to-side-rubbing-run and breast-pressing. When the female finally stopped running and stood still on straight legs, the male mounted her back. Maintaining his balance by fluttering, he jabbed at her head and frequently pulled her crown and nape feathers with his bill. Copulation occurred when both turned their tails; the actual contact lasted less than five seconds. Near the completion of the act, the female usually ran in small circles, eventually dislodging her mate. Then she ran off with feathers somewhat fluffed or, sometimes, crouched with feathers somewhat disarranged.

The entire act, from the time the male mounted until she dislodged him, was surprisingly long—40 seconds or more. One act, timed by Sutton counting slowly from one to 148, lasted at least two minutes; another, timed by Hampson with a watch, lasted fully three minutes and 25 seconds. The fact that these birds have such elaborate precopulatory and copulatory behaviors suggests the pair-bond is weak and needs constant reinforcing. The aggressiveness later helps split the pair-bond – which in Sanderlings occurs surprisingly early, before steady incubation takes place (see below).

The female Sanderling appears to take a major role in reinforcing the weak pair-bond. She usually follows the male about and vocalizes the most on the ground. When a strange female appears, she runs with feathers erected and tail spread, squatting with tail up in every depression she reaches in a concerted attempt to entice the male back. Even while she is running along the ground outside a scrape she utters the low, buzzing, typewriter-like notes described above. If her mate flies after a strange female, she follows, whereupon another kind of flight chase ensues that involves three birds.

Nest Sites

Many years ago Manniche (1910) described the nesting habitat of the Sanderling in northeast Greenland as "dry clay-mixed stony plains sparsely covered with *Salix arctica, Dryas octopetala, Saxifraga oppositifolia* and a few other scattered low growths." He stated that he never found nests on moors or on plains entirely uncovered though, apparently, he found the most nests on "stone-isles" which he described as scattered islands of stone and clay within the extensive moor-and-marsh stretches west of Stormkap. He thought that the distance from, and elevation above, the sea were of little consequence, but that the presence of freshwater lakes or ponds was significant.

Manniche's description probably suffices for many Sanderling nests in the Canadian Arctic archipelago. Most of the 14 nests, seen by us on Bathurst Island, and one each on Ellesmere and Jenny Lind Islands, were on stony, well-drained ridge tops (Figure 5), gentle slopes (Figure 6), or level alluvial plains (Figure 7), each with sparsely scattered willow, *Dryas,* and saxifrage plants –

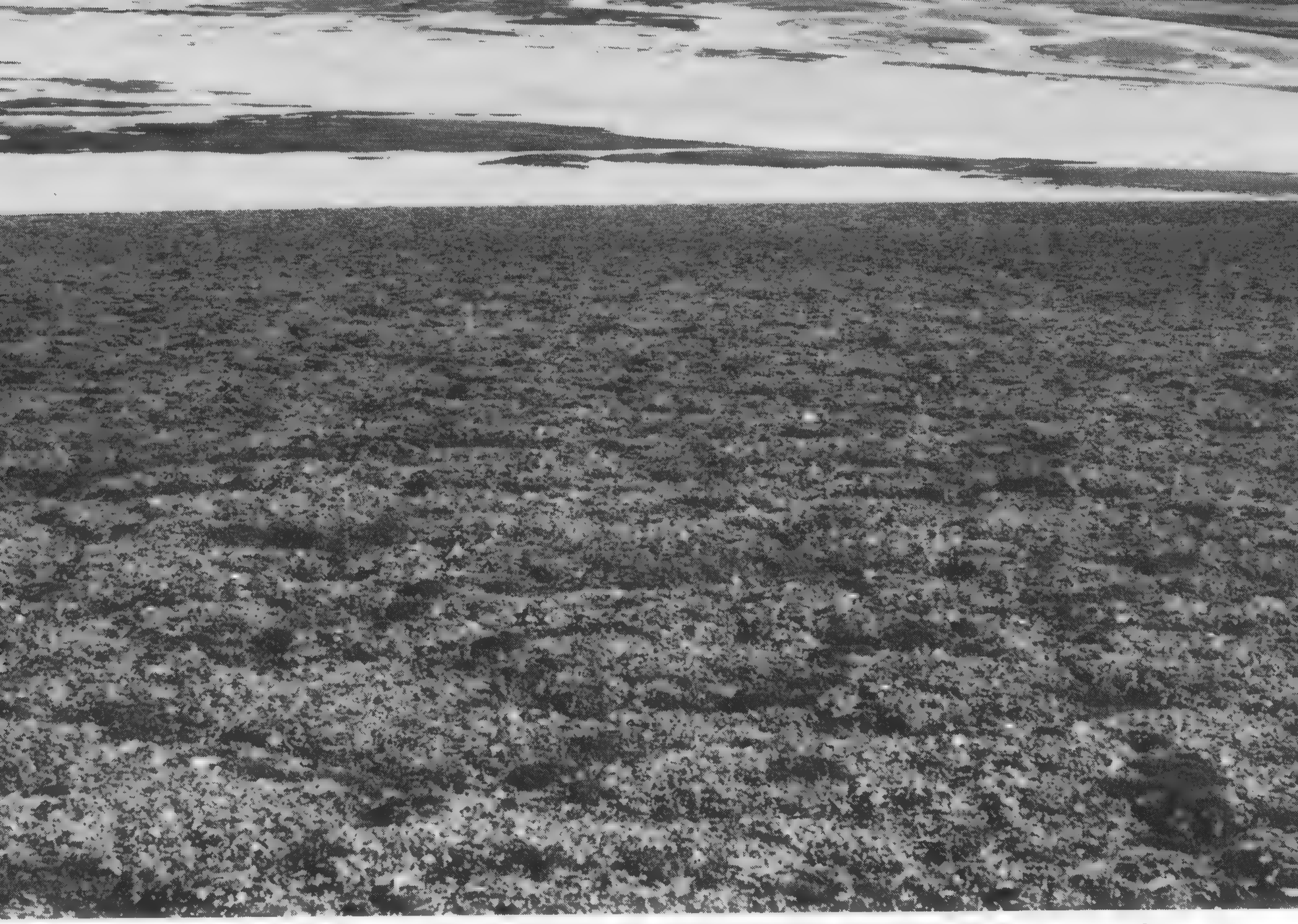


Figure 5. Nesting habitat of the Sanderling. One pair nested (number 13) in a clump of purple saxifrage on the fairly well vegetated, but nearly stoneless, ridge in the foreground. The banded male that incubated here in 1969 also attended eggs and young in 1968 at Nest 7, which at the time was two miles northeast in bluff country (upper right corner) beyond the broad, nearly snow-covered valley of the Goodsir River. Following the laying of the fourth egg at Nest 13, the clutch was abandoned for more than five days. The banded male suddenly reappeared and commenced incubating without assistance. The interval from laying to hatching of the fourth egg was surprisingly long—31.6 days.

essentially low-level dry tundra that was firm underfoot except for brief periods following the thaw. We found two nests on frost-heaved polygons with the ground soft and wet, thinly covered with scattered willow, and extensively enclosed by wet tundra and marshy ponds — hardly the expected spot for nesting Sanderlings.

On Bathurst Island in 1968, MacDonald collected plant samples in a typical Sanderling nesting area where probably less than 30 per cent of the ground had plant cover. Of the 21 species, *Saxifraga oppositifolia, Salix arctica,* and *Dryas integrifolia* were dominant. Of lesser importance were *Alopecurus alpinus, Festuca baffinensis, Poa abbreviata, Puccinellia angustata, Juncus biglumis, Luzula nivalis, Oxyria digyna, Arenaria rubella, Cerastium alpinum, Stellaria* sp., *Papaver cornwallisensis, Cardamine bellidifolia, Draba Bellii, Parrya arctica, Saxifraga caespitosa, Saxifraga cernua,* and *Saxifraga tenuis.*

Without exception all the Sanderling nests were in exposed situations, open to the sky and, although surrounded by barren, nearly sterile slopes in some cases, were within a few hundred yards of a marshy pond, and within a mile of extensive wet tundra. Most were below 200 feet elevation; one, on a rugged slope at least 500 feet in elevation, was close to marshy spots continuously receiving water from great banks of slowly melting snow.

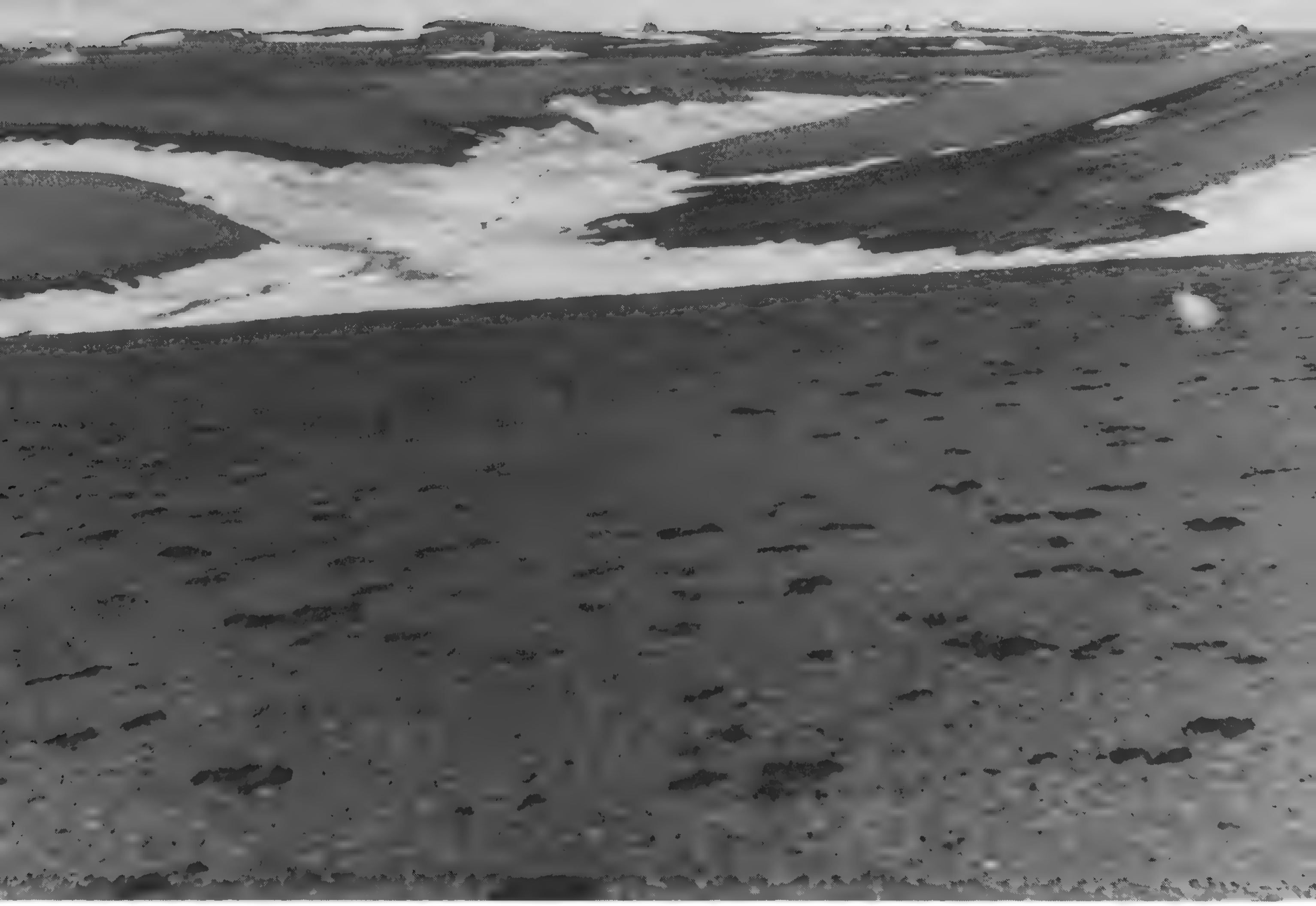


Figure 6 (*above*). Gentle slopes with scattered saxifrage, willow, and *Dryas* are readily utilized by nesting Sanderlings. Although the ground shown here is muddy during the period of egg-laying, it soon dries. The gullies close by provide the birds with wet feeding areas for many days. Musk-oxen, caribou, and hares (one at middle right) also frequent these slopes. A young hare nearly destroyed a Sanderling's egg when it accidentally stepped on the nest.

Figure 7 (*below*). Nesting habitat of the Sanderling. Nest 5 (1968) and Nest 14 (1969) were only 110 paces apart in dark patches of purple saxifrage on this flat, stony alluvial plain. Goodsir Inlet lies six miles eastward and beyond the bold, partly snow-covered ridge facing west in the background. King Eiders and Black-bellied Plovers also nested here. Knots preferred the barren ridge tops.

In 1968, we found the first Sanderling nest, with one egg, on 21 June in a snow-free spot of muddy ground where the ridge top all about was wet and covered with patches of soft snow, several of which were inches from the nest. By the time the clutch was complete on 25 June, all snow about the nest and nearly all on the ridge top had disappeared. Deep snow remained for many days in a gully and on steep slopes nearby.

We found other Sanderling nests that year with clutches completed and most of the snow in the nesting areas already melted. After examining each site with reference to lay of land and wetness of ground, and noting that other species, e.g., King Eiders (*Somateria spectabilis*) and Black-bellied Plovers (*Squatarola squatarola*), laid eggs in exposed, muddy spots near melting snow in the same areas, we concluded that most, but not all, of the Sanderling nests probably had been close to soft snow during egg-laying. In 1969 we found the first Sanderling nest, with one egg, on 25 June on a muddy slope where snow was rapidly disappearing.

In 1968 the tardy nesting of one Sanderling may have been the result of a stubborn thaw and persistent snow cover. The nest, one of two on polygon ground enclosed by marsh and collected on 11 July along with the attendant bird, contained fresh eggs when other Sanderling eggs were much advanced. The ovary of the female had only four ruptured follicles, indicating that the bird was not renesting. Because the marsh in which this nest was situated had deep snow and ponds nearly frozen shut as late as early July, so far as we knew, no birds of any species nested there. Possibly some shorebirds, like many waterfowl, are so tied by tradition to nesting places that they delay or skip nesting altogether in years when their favored breeding spots fail to open up.

The hypothesis may partly explain why Sanderlings and other shorebirds do not use the many seemingly suitable snow-free areas soon after their arrival. Sanderlings probably did not lay eggs much before 16 June on the Bathurst breeding ground in 1968 although nearly two weeks had passed since their arrival on 3 June. And most birds waited until after 20 June despite the fact that there were extensive low-level dry tundra areas open in early and mid-June. Egg-laying started even later in 1969.

Selection of Nest Site

In 1968 we failed to note a Sanderling selecting a nesting spot, having been repeatedly led astray by the birds' activities at precopulatory scrapes outside of nesting areas. On 25 June 1969 we witnessed the selection of a nest site by a pale female whose bright mate was a bird we had banded at a nest the previous year.

Sutton and Taylor first saw the pair on a slope a mile and a half west of camp. Although we had seen no precopulatory activity, the birds engaged in what appeared to be successful copulation at about 12:00 hours. For the next three hours I followed the birds about the slope, recording activities that were anything but typical of precopulatory behavior.

Without making any attempt to attract the male through vocalizations or body postures, the female settled in depressions or hollows in the turf on six different occasions, each time fluffing out her feathers as though she were settling on eggs, and usually remained less than a minute. She twirled, tossed bits of material out of the hollow, and, at least once, scratched out material with her foot. Several times the male attempted copulation, indicating that the very presence of a female in a hollow is at times stimulus enough to elicit response. All but perhaps one of his attempts were, however, quickly aborted by the female which simply failed to respond.

At 15:00 hours the female settled in a hollow and remained there for five minutes, leaving only once for a few seconds. She settled down so comfortably within this hollow that I at first believed she had a full complement of eggs; there was not one. Finally, the male ran up and pried her out with his bill. He then attempted a side-to-side-rubbing-run, and even copulation, without success. Several hours later she laid the first egg of a four-egg clutch in this very hollow (Nest 13).

Nests

According to Manniche (1910), the Sanderling in northeast Greenland nests at the edge of, or in, a tuft of *Dryas*. He stated that the bird formed a cup-shaped hollow, not very deep and sparsely lined with withered leaves of *Salix arctica* or other plants growing in the vicinity. He further stated that the situation of the nest, like that of the nesting habitat, was extremely constant. J. H. McNeile (*in* Bannerman, 1960) reported that all nine Sanderling nests, found on Spitsbergen during 1931–1932, were filled with the "brown Arctic willow leaves."

The nests we found on Bathurst Island were similar, except that six nests were in *Salix,* five in *Saxifraga* (Figures 8 and 9), and only two in *Dryas*. Most were partly filled with dry, withered saxifrage or willow leaves mixed with lichens, chiefly *Thamnolia vermicularis,* bits of moss, and occasionally dry willow twigs and pebbles. Taylor found a nest on 13 July 1969 in a "frost crack" on bare ground near a saxifrage. On Ellesmere Island I saw a nest in *Dryas* which was partly filled with dry willow leaves; on Jenny Lind Island I saw another in a slight depression in a bare spot, partly filled with dry willow leaves and lichens.

Sanderlings enlarge nest hollows even before egg-laying, but whether they ever line or add material to the hollow is questionable. I believe that in some cases Sanderlings simply drop the first egg in a depression, be it ever so slight; and that they enlarge the depression gradually during egg-laying and incubation. I believe also that most, if not all, of the plant material that partly fills the cavity accumulates through accident rather than through any deliberate action on the part of the bird. McNeile (*in* Bannerman, 1960) observed some Sanderling scrapes that were very shallow; one looked as if it might have been an old Purple Sandpiper's—an observation further suggesting that eggs are simply dropped into depressions without much scrape-building on the part of the Sanderling.

The Bathurst Island nests, especially those situated in willows, were slight, rather crude depressions in which dry leaves accumulated through wind action or some other disturbance. At most of these nests green willow shoots grew through the dry linings of leaves by the time the eggs hatched.

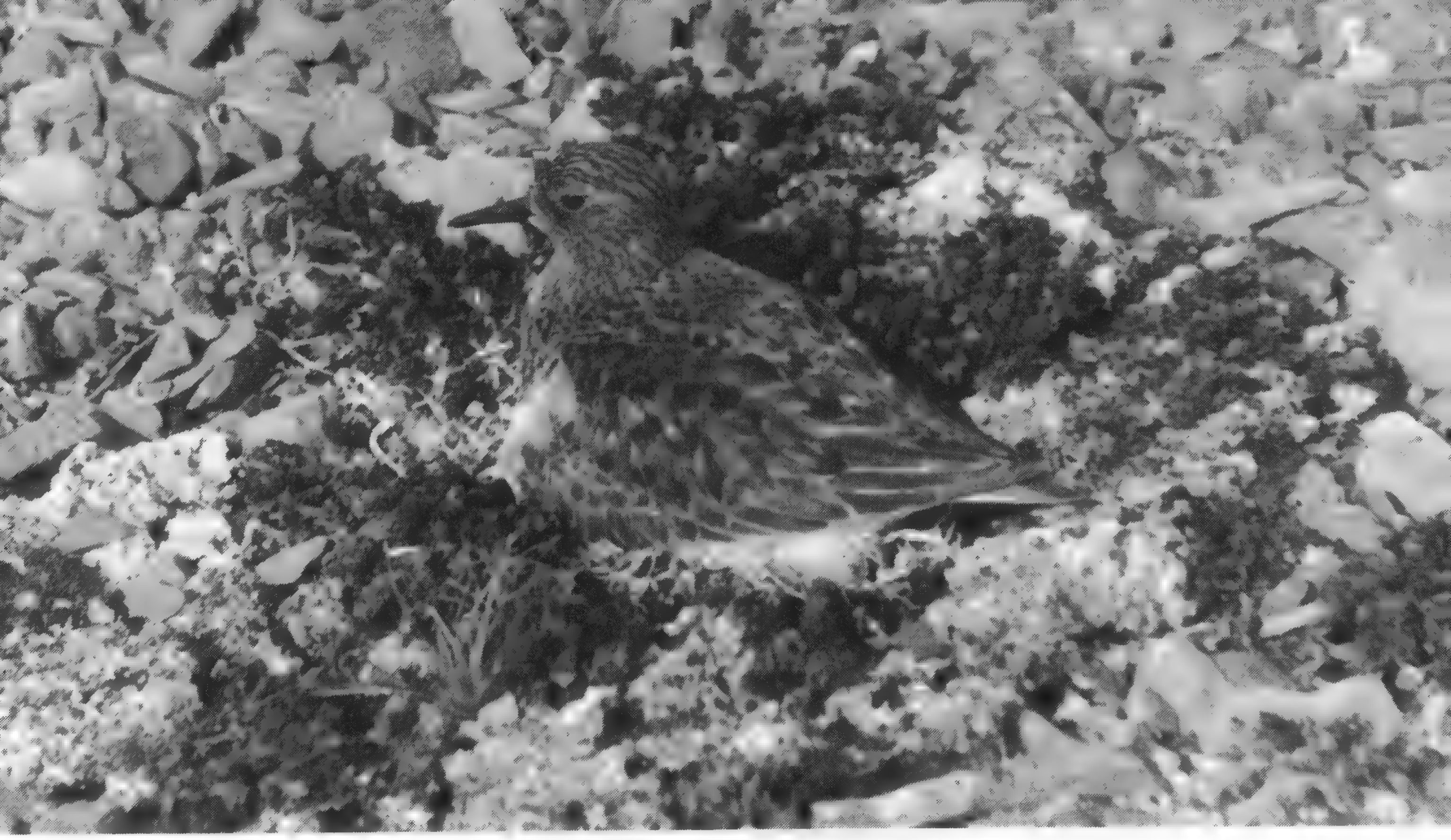


Figure 8. Incubating male Sanderling at Nest 5 in purple saxifrage on the stony alluvial plain six miles west of Goodsir Inlet on 3 July 1968. We trapped and banded this individual (partial Band Number 125101) at this nest which was later destroyed by a predator. The banded bird returned in 1969 and nested close by (see **Figure 9**). Although we believed that it was a male from the start, the sex was not proven until it was collected at Nest 14 on 28 June 1969. The summer feathers of this bird were so bright that Sutton decided to use the specimen as his model for the Sanderling painting (Plate I).

Nest 2 on Bathurst Island, in a small clump of purple saxifrage, was atypical in that it was filled exclusively with the white lichen that overflowed the saxifrage onto the bare ground beside it. On 21 June the nest contained only one egg partly buried in the loose lichens, leading us to believe at first that the bird had covered its egg. This was not the case.

We found this nest (Nest 2) by watching an adult Sanderling, believed to have been a male, that walked to the saxifrage clump and deliberately poked and tossed lichens and what appeared to be a large chunk of saxifrage into the air. Then it settled down on that very spot and turned several times before running off. This happened some 10 hours after the first egg had been laid. Throughout egg-laying, and right up to the end of incubation, the Sanderling gradually modified and somewhat enlarged the hollow. Even the lichens on the ground immediately adjacent to the saxifrage were removed in time. Taylor, who scattered additional lichens around Nest 2 on 17 July, saw the parent bird remove these lichens within a few hours time. The result of this activity was a neat cup of white lichens that contrasted sharply with the dark saxifrage. Significantly the bird never added any dry leaves to the nest during the long period of observation.

Egg-laying Period

Following discovery of the first egg at Nest 2, at 23:30 hours on 21 June 1968, I checked the site regularly at one- to two-hour intervals. The second egg was laid between 17:00 and 18:30 on 22 June. Up to that time we had not seen any Sanderlings on or near the nest, which appeared undisturbed; lichens still partly covered the single egg.

The two eggs were fully exposed. We covered them with lichens and they remained concealed until at least 21:30 the following day, indicating that no bird had been on the nest for 27 hours. By 22:20 the eggs had been moved and exposed.

The female laid the third egg between 23:15 and 23:25 on 23 June, making the interval between the second and third eggs 29 hours, 35 minutes (±50 minutes). The pair had made no attempt to cover the three eggs. Still, the Sanderlings did not incubate, though at least one bird visited the nest a few times up to the laying of the fourth egg. Of this we were certain for each time that we covered the eggs, the returning bird uncovered them and moved them as well.

The bird laid the fourth egg between 02:15 and 03:15 on 25 June, making the interval between the third and fourth eggs 27 hours, 25 minutes (±35 minutes). Steady incubation commenced after completion of the clutch. We did not determine when it actually started.

In 1969 we observed egg-laying at Nest 13, which was empty when first discovered at 15:00 hours on 25 June, and had the first egg by 22:45 that same day. Very likely it had been laid during the period from 21:00 to 22:45, since the second egg appeared sometime from 01:45 to 02:15 on 27 June. The interval between the first and second eggs was at least 27 hours.

We saw laying of the third and fourth eggs in Nest 2 from a blind. The female arrived at the nest at 05:05 hours on 28 June. After fluffing her feathers

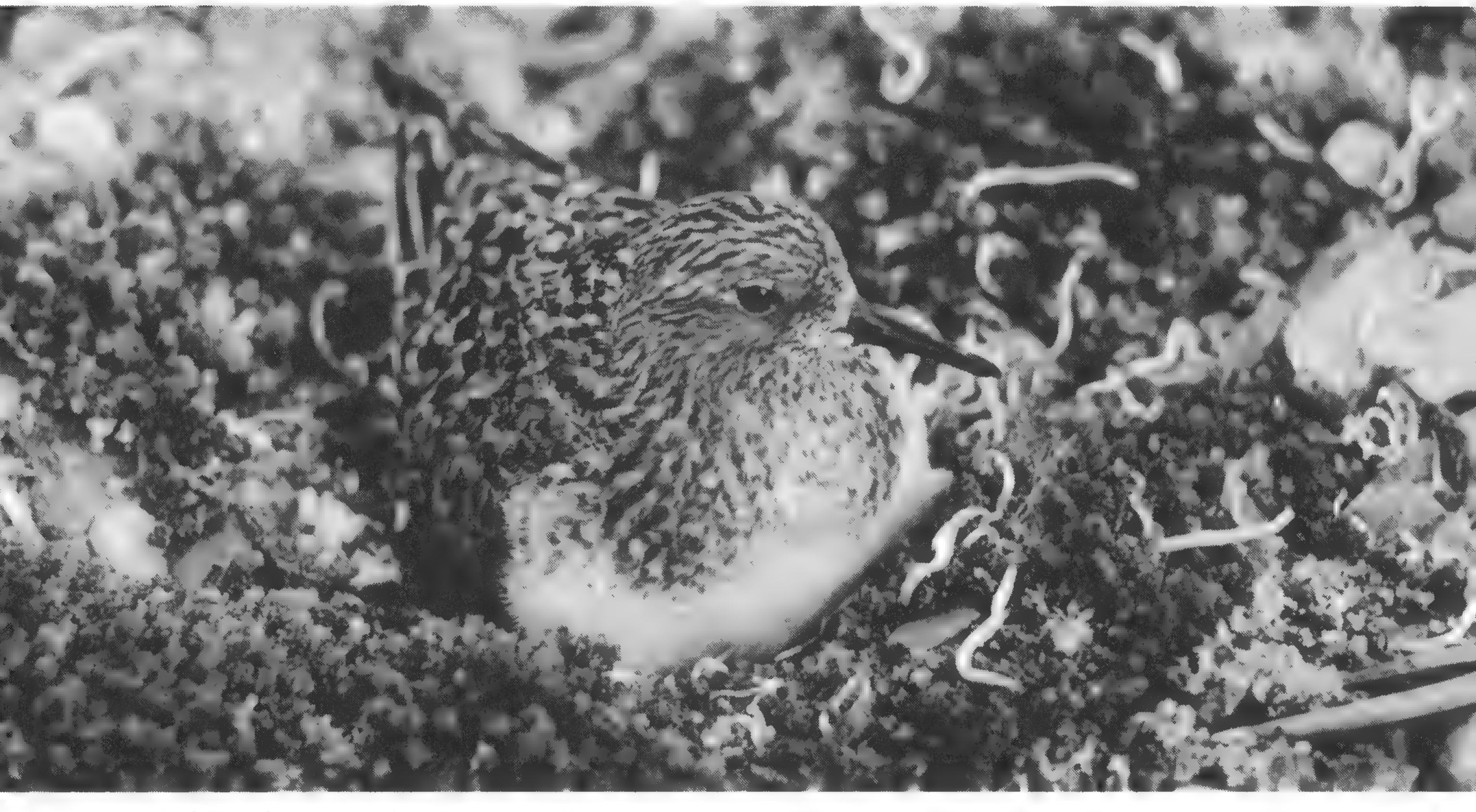


Figure 9. Incubating male Sanderling at Nest 14 on 28 June 1969. This same male nested 110 paces away during the previous summer (see Figure 8). Females may enlarge the nest cup before and during egg laying; and at any given nest the one incubating bird, either male or female, may further enlarge the cup. Nothing is added although bits of plants, usually dry leaves and lichens, fall into the cup through the movements of the bird or wind action. The white, wormlike lichens (*Thamnolia vermicularis*) that adorn the saxifrage and surrounding stones are everywhere common on the Bathurst breeding ground.

and changing her position several times, she stood up, stretched, and no doubt laid her third egg at 05:40 when she wobbled noticeably. After that time she turned around frequently, preened, and probed at the vegetation outside the nest cup until we flushed her at 05:58. The interval between the second and third eggs was 27 hours, 40 minutes (±15 minutes).

On 29 June the female ran into the nest at 07:26 hours and probably laid her fourth egg at 07:48, leaving the nest when flushed at 08:25. As before, there had been much turning, arranging of feathers, and probing outside the nest cup, especially after the egg had been laid. The interval between the third and fourth eggs was close to 26 hours, 28 minutes.

Except for those times when the female went to the nest to lay, neither adult visited the nest, so far as we could determine. Actually we failed to find the birds anywhere within a mile of the nest.

The 26- to 29-hour interval between eggs of a Sanderling clutch, a period heretofore not ascertained precisely, falls close to that of other small to medium-sized tundra sandpipers (Parmelee *et al.*, 1967). A nest found by J. H. McNeile (Dalgety *et al.*, 1931), with one egg on 27 June and four eggs on 30 June, led to the belief that Sanderlings lay daily. His notes (*in* Bannerman, 1960) about finding a nest with four eggs (two were "dead fresh, one was just a day or two set, and the other touched with a slight spot of red") on 12 July 1932 suggest that incubation started before completion of the clutch. We question whether incubation actually starts before completion of the clutch in Sanderlings.

Wholly unexpected at Nest 13, however, was an interval of five days and 16 hours between the completion of the clutch on 29 June (07:48 hours) and start of incubation near midnight of 4 July (23:55 hours). Throughout this time, Gray and Lamothe continually checked the eggs and found them exposed and cold. Both men were convinced that the adults had totally neglected the nest – as indeed they had, a fact confirmed later when Gray, Lamothe, and Taylor computed the incubation period for Nest 13 as 31 days – exceedingly long for a Sanderling.

Eggs

Jourdain's description of Sanderling eggs in Witherby *et al.* (1940) is as good as any in the literature: normally four eggs, but three recorded exceptionally; shape pointed ovate or subpyriform; hardly any gloss; ground color dull greenish olive as a rule, ranging to olive-brown and exceptionally greenish blue; rather sparsely marked with small irregular brown spots and shell-marks, generally heavier at big end and at times all concentrated there, sometimes a few fine blackish spots or streaks. We should stress that the eggs quickly lose much of their green color and turn brownish, especially when blown, as Pedersen (1942) stated. No doubt the fading in preserved specimens has led some writers to believe that the eggs are much less colorful than those of other shorebirds. P. Matthiessen (*in* Stout *et al.*, 1967), for example, called Sanderling eggs "exceedingly dull." Obviously, he had never seen a fresh Sanderling egg.

In the 60 live Sanderling eggs, including 52 on Bathurst Island, that I have seen in Canada, there was great variation, not so much in size and shape as in markings and especially in ground color. To be sure, some eggs were dull greenish with few markings of any kind, but most were handsomely embellished with small spots and various other markings, chiefly around the large end, often forming a distinct wreath, on a ground color ranging from pale dull green to the brightest green imaginable. The ground color of some was brownish green and of one clutch pure olive. The eggs in Nest 2 were the greenest of the more than forty kinds of live wader eggs I have ever seen. All four approached an emerald green and contrasted sharply with the white lichens that lined the nest. The fresh green color that makes the Sanderling's egg outstanding starts to fade the day the egg is laid and continues to fade throughout incubation so that much color is lost by hatching time. Whether fading—possibly correlated with change of season — has cryptic value is uncertain. Blowing the egg apparently speeds the fading, but no one has studied this. The few egg specimens we prepared all faded to some degree. The clutch size in all nests, seen by us in Canada, was four except for one nest found on 13 July 1969. That clutch of two eggs, one with a dented shell, very likely had been reduced through predation.

Incubation Period

Since Manniche (1910) stated that the "time of incubation is 23 to 24 times 24 hours" for Sanderlings, numerous references have given the incubation period as 23 to 24 days. Manniche, without giving any information on how he arrived at these figures, further confused the issue by stating that the first nest he found held eggs that already had been incubated for some days. He collected six of 11 nests he found and at least one had heavily incubated eggs. Presumably he did observe one nest with an incomplete clutch, perhaps a clutch he thought to be fresh.

Today, the usually accepted meaning of the incubation period is the time interval between laying and hatching of the last egg of the clutch. In Nest 2, found with only one egg in 1968, we marked each egg of the four-egg clutch and ascertained the period from laying to hatching of the fourth egg, as shown in Table 1. The fourth egg laid hatched first, and the incubation period for this nest was 24 days, six hours, 15 minutes (±30 minutes).

In 1969 the incubation period of Nest 13 is shown in Table 2. The "official" time for Nest 13 is 31 days, 16 hours, 46 minutes (±34 minutes), quite a contrast from that of Nest 2.

Although we do not know the minimum time required for incubation, we can say that some Sanderling eggs hatch in less than 25 days. Even the delay of five days and 16 hours, from completion of the clutch to start of incubation, does not fully account for the long period of incubation at Nest 13 because the period from the apparent start of incubation on 4 July (23:55 hours) and hatching on 31 July (00:00–01:07) was more than 27 days! This can only mean that either steady incubation did not actually commence until after 23:55 hours on 4 July, or the development of embryos was in some manner retarded during the period. Perhaps both factors contributed to what appears to be a remarkable variability in the incubation period of this species.

TABLE 1

Duration of Incubation in Sanderling Nest 2

Egg number	*Time laid*	*Time hatched*	*Total time in nest*	*Time from laying of fourth egg*	*Young number*
1	21 June	21:41 19 July		24 days, 18 hrs., 56 min. (±30 min.)	4
2	17:00-18:30 22 June	09:30 19 July	26 days, 15 hrs., 40 min. (±45 min.)	24 days, 6 hrs., 45 min. (±30 min.)	2
3	23:15-23:25 23 June	16:00 19 July	25 days 16 hrs., 40 min. (±5 min.)	24 days, 13 hrs., 15 min. (±30 min.)	3
4	02:15-03:15 25 June	09:00 19 July	24 days, 6 hrs., 15 min. (±30 min.)	24 days, 6 hrs., 15 min. (±30 min.)	1

TABLE 2

Duration of Incubation in Sanderling Nest 13

Egg number	*Time laid*	*Time hatched*	*Total time in nest*	*Time from laying of fourth egg*	*Young number*
1	before 22:45 25 June	08:50-12:15 31 July	at least 35 days, 10 hrs., 5 min.	32 days, 2 hrs., 45 min. (±103 min.)	4
2	01:45-02:15 27 June	06:00-06:58 31 July	34 days, 4 hrs., 29 min. (±44 min.)	31 days, 22 hrs., 41 min. (± 29 min.)	3
3	05:40 28 June	01:07-01:10 31 July	32 days, 19 hrs., 27 min. (± 2 min.)	31 days, 17 hrs., 21 min. (± 2 min.)	2
4	07:48 29 June	00:00-01:07 31 July	31 days, 16 hrs., 46 min. (±34 min.)	31 days, 16 hrs., 46 min. (± 34 min.)	1

Role of the Sexes during Incubation and Fledging Periods

The most puzzling aspect of the Sanderling's breeding behavior concerns the role of the sexes in care of eggs and young. On this point authors are argumentative but not lucid. Manniche (1910) thought that females alone incubated eggs and attended young. He presented such a strong case for this viewpoint that he exercised considerable subsequent influence. Bird and Bird (1941), who found upward of a dozen Sanderling nests in Greenland during 1937–1938, did not record any males at nests, though they believed that males may have in some way assisted in the late stages of incubation and the brooding of young (male seen brooding). Of eight birds shot at nests by Pedersen (1942), all were females. Witherby *et al.* (1940) state that male Sanderlings do not possess incubation or brood patches.

Contrary to these views, Feilden (1877) collected a male at a nest as early as 1876, as did Madsen (1925). Manning *et al.* (1956) collected a male with brood patches and another with young. H. Walter (*in* Bent, 1927) believed that both sexes hatched eggs, and G. Kolthoff (*in* Loeppenthin, 1932) thought that both parent birds attended the young. Godfrey (1966) summed up present-day thoughts on the subject, stating that the female definitely incubates and opinions differ regarding assistance of the male.

These statements, plus the fact that only one adult, probably a female, was seen during limited observations at an Ellesmere Island nest and a lone male with distinct brood patches attended young in the same area, led Parmelee and MacDonald (1960) to believe that both sexes incubate, but that one parent, either the male or female, at a given nest deserts at some point in the cycle. We still adhere to this view and present new evidence below.

It appears that one of the pair deserts by the time incubation begins. At Jenny Lind Island, during a nearly 24-hour-long watch at a Sanderling's nest with fresh eggs, only one adult incubated. The bird, a pale female, was shot by Sutton for positive sex identification (Parmelee *et al.*, 1967). At the Bathurst breeding ground on 25 June 1968, I collected a bright male with swollen testes and distinct brood patches at a nest where the eggs were only slightly incubated. On 11 July, I shot a pale female with ruptured follicles and distinct brood patches at a nest with fresh eggs. I looked for the mates of these two birds but did not find them.

Convinced finally that males do incubate, we all set about looking for nests for the purpose of observing incubating birds. In 1968 we succeeded in trapping and color marking the incubating adult at eight nests; two of these birds, banded at Nests 5 and 7, we observed again in 1969 at Nests 13 and 14, respectively. Data concerning the ten nests are presented in Table 3.

In the species of sandpipers in which the sexes share the incubation, it is usually simple to trap both birds of a pair at the nest. Not only did we fail to trap two birds at a Sanderling's nest, we also failed to see two birds at a single nest following egg-laying. We were always on the lookout for both and especially watchful during and immediately following the hatching of young, yet no mate ever appeared during these crucial times at any of the six nests where we observed the hatching. The male or female parent, which alone had incubated the eggs, also raised the brood. We found no exception.

Unfortunately, once the marked adults and broods had left the nest, we lost track of them. We do know, however, that the banded adult from Nest 2 was still the only bird attending when the brood was one week old; and that the banded adult from Nest 12 was the only one attending when its brood was more than two weeks old.

We saw only one adult attending unmarked broods on the Bathurst breeding ground in 1968. On 17 July we banded a pale adult, probably a female, and four downy chicks not long out of the nest. This adult alone attended the brood when we saw them on 18 July and on 25 July. Sightings of unmarked Sanderlings with broods are given in Table 4.

What seemed at first to be an exception to the one-parent-one-brood rule later appeared to be false. A bright individual and a pale individual ran at the edge of a marshy pond where two small young hid on 27 July. Further observation on 28–29 July convinced us that only the bright individual attended the chicks. We never saw the pale bird approach them. Possibly the gray bird had young of its own nearby; or possibly it, like several Knots, was attracted to the area by our disturbance, or perhaps, having lost its own eggs or chicks, it was attracted to the brood – as sometimes happens with White-rumped Sandpipers and some other shorebirds.

How the complex behavior in which the pair-bond suddenly dissolves comes about prior to incubation, and what adaptive value this behavior can possibly have, is a question for which we have no answer at present. The solution to the puzzle may lie in the long period between completion of the clutch by the female and start of incubation by the male, such as the more than five-day period at Nest 13. The nesting period is so short in the arctic summer that the birds must have been doing something constructive during this time. Conceivably they were at another nest, one which the female incubated, allowing the male to return to the first. The idea of sampling predation, as attractive as it may be with some species, does not quite fit the Sanderling, though it cannot be ruled out altogether. Sampling predation implies survival value for a nest site that escapes predation during a period following laying when the eggs are left unattended (see Drent, 1967).*

Behavior of Incubating Adult

The most convincing evidence that one bird alone incubates and cares for the brood came during the day-by-day, round-the-clock observation that started at Nest 2 at 15:00 hours on 5 July 1968 and continued without letup until 23:17 on 19 July – a period of 14 days, eight hours, 17 minutes. The incubating bird, believed from the first to be a male, was trapped and marked at 17:30 on 7 July. Up to that time we had some doubt whether the same bird that flew off periodically returned each time. Following the banding there was no doubt. Only the banded bird incubated and later attended the brood – at least throughout our period of careful observation.

A number of noteworthy observations concerned with incubation came to light during the continuous watch at Nest 2. Inasmuch as one bird alone

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*Special note: Each ovary of two nesting Bathurst females, taken by me in 1970 and later examined critically by R. B. Payne, showed clear evidence of ovulation of two clutches in quick succession.

TABLE 3

Sex of Incubating Sanderlings

Nest number	*Probable sex of banded bird*	*Period of observation following banding*	*Number of observations of banded bird on nest*	*Number of observations of an unbanded bird on nest*
2*	male	7-19 July**	379	0
5	male	2- 4 July	9	0
6	?	3- 4 July	3	0
7*	male	16-24 July	12	0
8*	male	10-17 July	19	0
9	female	10-21 July	14	0
11*	female	13-21 July	7	0
12*	male	15-19 July	4	0
13*	male	5-31 July	30+	0
14	male***	28 June	1	0

*Hatching period observed.

**Continuous round-the-clock observation.

***Collected at nest with fresh eggs on 28 June. The mate, seen on 22 June, was not found on 28 June.

TABLE 4

Sex of Adult Sanderlings with Broods

Sex of adult	*Number of young*	*Date*
Female*	3	19-20 July
Female*	4	27 July
Female**	2	28 July
Female*	2	30 July
Female*	4	31 July
Female**	1	3 August
Male**	2 recently fledged	7 August
Male**	1 nearly fledged	8 August

*Probable sex.

**Sex confirmed by collecting.

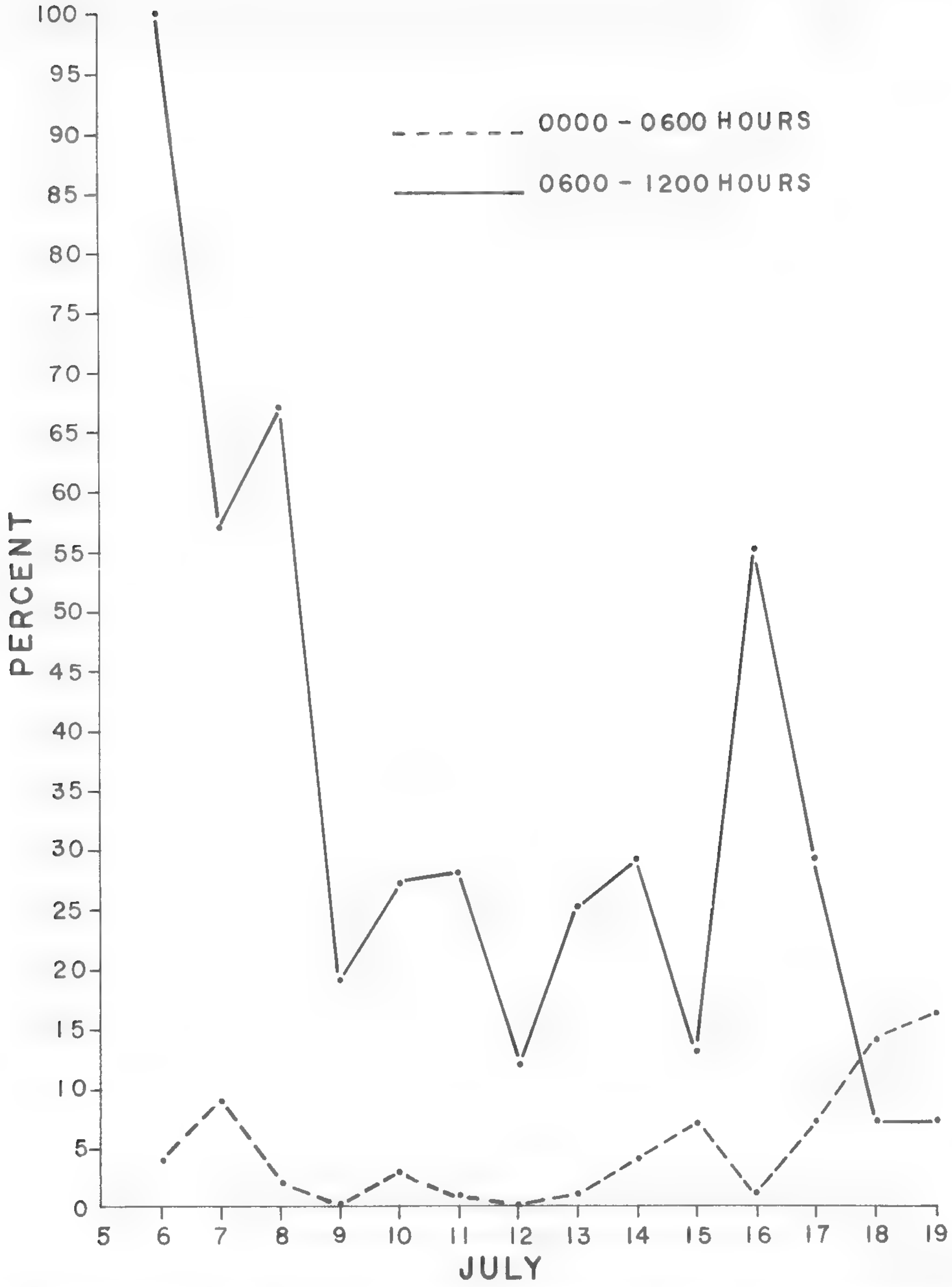

Figure 10. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during the morning hours of 6–19 July. The broken line indicates the early morning period 00:00–06:00, the solid line, the later period 06:00–12:00. The incubating Sanderling usually remains on the nest during the cool early morning hours (up to 06:00). The inattentive periods rise sharply during the later hours of the morning.

incubated, we especially wanted to know just how much time the bird spent off the nest during any one day and for the entire period. We kept an accurate record of when the parent bird left and when it returned to the nest. Although we occasionally failed to see the bird arrive or depart, the error in these cases was slight, for at no time was an eye off the nest for more than a minute or two. We did not count the times we flushed the incubating adult from the nest for routine egg checks because then the conditioned bird moved away only a few feet and invariably returned to the eggs as soon as we retired.

Figures 10 and 11 show graphically the percentage of time that the incubating Sanderling was away from the nest during 5–19 July.

As seen in Figure 10, the incubating Sanderling remained mostly on the nest during the cool early morning hours (00:00–06:00). The average time away was only 5 per cent; it left the nest 46 times for a total of 237 minutes; and each trip lasted from one to 27 minutes, averaging 5.1 minutes.

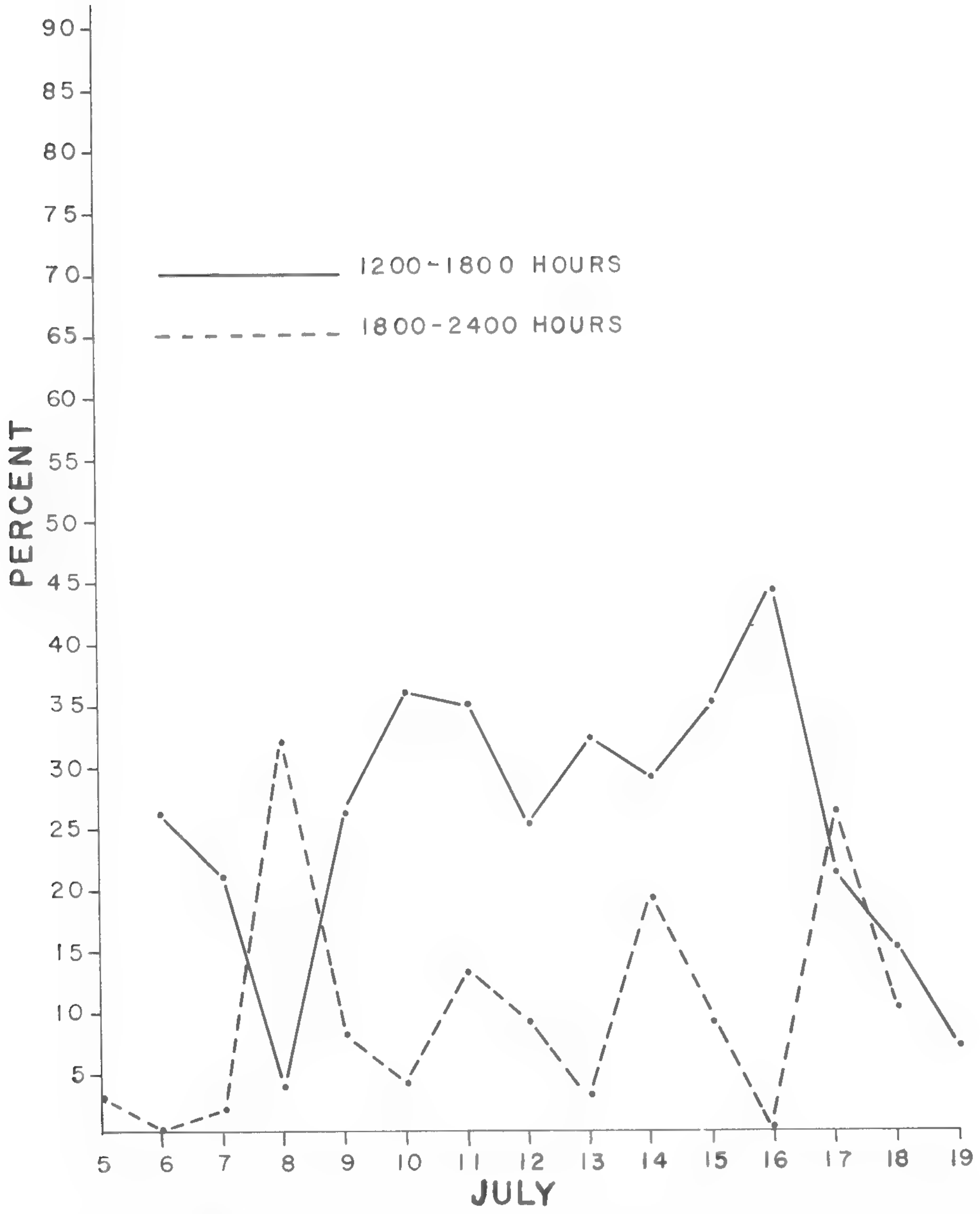

Figure 11. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during the afternoon hours of 5–19 July. Solid line indicates the afternoon hours 12:00–18:00 for 6–19 July, the broken line, the later period 18:00–24:00 for 5–18 July. Each inattentive period averaged nearly the same number of minutes during both periods (8.5 and 8.2 minutes); but the number of trips off the nest between midday and 18:00 hours was almost three times more than between 18:00 hours and midnight (151 to 58 trips, respectively, during the two-week period).

During the late morning hours (06:00–12:00), the Sanderling's time away was from seven to 100 per cent of each six-hour period and averaged 34 per cent for the total time. The bird left the nest 116 times for a total of 1,719 minutes, each trip lasting from one to 360 minutes and averaging 10.1 minutes. The long absences from the nest on 6, 7, 8, and 16 July, shown by the high points on the graph, increased the average time considerably.

Though these high points show that the Sanderling left the nest for unusually long periods, they do not show the longest periods when the times overlapped the observation periods. For example, on 6 July it was off for 454 consecutive minutes, from 05:46 to 13:20; on 7 July, 219 minutes, from 05:33 to 09:12; on 8 July, 223 minutes, from 08:21 to 12:04; on 16 July, 333 minutes, from 09:04 to 14:37. These figures stand out when compared to those for all other times when the bird was never off the nest for more than 20 minutes. See Table 5 for daily timing of periods on and off Nest 2 from 6 to 19 July.

The occasional long absences from the nest are puzzling. In 1966, on Jenny Lind Island, we noted this phenomenon at a Sanderling nest and, also, at the nests of White-rumped Sandpipers where the female alone incubates the eggs. Although these birds generally sit tight during cool or inclement hours, this is not always the rule. Nor do the long absences seem to depend on weather conditions or human disturbances. Whatever the explanation, the embryos within the chilled eggs somehow survive.

As seen in Figure 11, the incubating Sanderling was off the nest from four to 44 per cent (average 25 per cent) of the time during the afternoon hours 12:00 to 18:00 for 6–19 July. It left the nest 151 times for a total of 1,291 minutes, averaging 8.5 minutes per trip. Discounting the long absences in the previous period, the graph indicates that this is an important feeding period.

TABLE 5

Day-by-day, Round-the-clock Timing of Incubation at Sanderling Nest 2

Date in July	*Minutes on nest*	*Minutes off nest*	*Number of times off nest*	*Per cent of time off nest*	*Minimum number of minutes off nest*	*Maximum number of minutes off nest*	*Average number of minutes off nest*
6	966	474	4	33	3	454	94.8
7	1119	321	17	22	1	219	18.8
8	1061	379	13	26	3	223	29.1
9	1254	186	27	12	2	13	6.8
10	1189	251	28	17	1	19	8.9
11	1159	281	31	19	1	19	9.0
12	1273	167	20	12	1	14	8.3
13	1218	222	30	15	1	11	7.4
14	1170	270	41	12	1	20	6.6
15	1207	233	35	16	1	16	6.7
16	1084	356	6	24	1	333	59.3
17	1141	299	45	21	2	14	6.6
18	1273	167	35	12	1	8	4.8
19*	1280	160	36	11	1	17	4.4

For the period 6-19 July:
Total time on nest: 16,394 minutes
Total time off nest: 3,766 minutes or 19 per cent
Total number of times off nest: 368
Average time away from nest per trip: 10.2 minutes
Average number of trips per day: 26.2

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*Since continual observation at Nest 2 terminated at 23:17 on 19 July, it is only assumed that the bird was on the nest from 23:17 to 24:00 that day.

For the cooler hours 18:00–24:00, the incubating Sanderling was off the nest from zero to 32 per cent of the time during 5–18 July, averaging only 9 per cent. The bird left the nest 58 times for a total of 477 minutes, averaging 8.2 minutes per trip.

Data concerning the 24-hour day at Nest 2 for the period 6–19 July are graphed in Figure 12.

The total time (19 per cent) off the nest for the period 6–19 July would be somewhat less if it were not for the few times the bird was away for unusually long spells on 6, 7, 8, 16 July. Nevertheless, 19 per cent is the actual time spent off the nest for a definite period prior to successful hatching. This figure compares well with similar nest-relief of the White-rumped Sandpiper. With much less data at their disposal, Drury (1961) and Parmelee *et al.* (1968) roughly estimated that females of that species are off the nest 20 to 30 per cent of the time.

The marked Sanderling left Nest 2 to feed, to pursue other Sanderlings, and to avoid birds and mammals, including predators. Most trips involved feeding.

The bird often flew north and fed along a small, melt-water creek that flowed southeastwardly some 200 yards from Nest 2. Other Sanderlings and some Knots also probed in the mud along this creek bed and slopes that rose gently from its banks. We were unable to determine precisely what food they found there.

Almost as often, the marked bird flew southeast, disappearing over the bank of the creek, doubtlessly following the creek bed down to a big marsh a quarter of a mile below the nesting ridge. Sometimes it flew straight down the precipitous south bank of the ridge and probed near the edge of a huge snow drift. Although at times it ran from the nest, when it went off to feed, it almost invariably flew directly from the eggs or chicks for about 30 to 50 feet and then suddenly gained some altitude before dropping down to the feeding spot.

On occasion it rose very rapidly, descended, rose again, and then plunged in an undulating performance; or it suddenly flew off twisting and turning. Once it did a quarter barrel-roll and the flight that began as a feeding excursion evidently developed into something else, possibly due to the presence of another Sanderling. Essentially, the feeding flight was direct.

Rarely, when the wind was not blowing hard, the marked Sanderling rose on rapidly beating wings straight up from the eggs before leveling off a foot or so above ground. MacDonald noted that the bird on leaving the nest in periods of low wind, "raises so legs are only about half straightened, then whirrs wings and rises almost vertically for about 12–18 inches." I once saw the bird rise a foot above the eggs, suddenly turn 180 degrees, and fly off in the opposite direction.

Returning to the nest was less spectacular. Nearly always the bird flew in on shallow wing-beats low above the ground, alighted one to 20, usually five to 15, feet from the nest, ran directly to the eggs or chicks, and sat without any preparatory behavior. At times the bird ran in from greater distances—as much as 125 feet. Never did we see this bird, or any Sanderling, flutter down on the eggs in the manner so characteristic of turnstones.

Most feeding trips lasted from three to 10 minutes and some barely a minute, hardly long enough for the bird to take a drink. Whether eating or drinking, it returned with a wet bill that sparkled on clear days.

The manner of feeding, seen so often at Nest 2, did not differ much from that observed at other Sanderling nests. The marked adult at Nest 7 fed briefly at a wet spot only 240 paces from the eggs. The one at Nest 8 flew a quarter-mile to feed for a few minutes at a marshy pond. The bird at Nest 11 flew a quarter-mile to a marshy pond and, during rapid-fire feeding there on 14 July, plucked insect larvae from water one to three inches deep.

The number of Sanderlings that visited the immediate vicinity of Nest 2 was astounding. We felt that quite a few of these birds were aware of Nest 2 because at times they ran up to or flew close to it. The incubating Sanderling reacted to these intrusions in various ways. Sometimes it crouched or flattened out on the nest, as it often did when a predator approached; sometimes it paid little or no attention to an odd Sanderling or even a flock; most of the time it flew at the intruders and chased them hard with some chases ending in genuine confrontations. We saw no less than 56 intrusions on the *sanctum sanctorum* of Nest 2.

Most intrusions were by single individuals, some of which visited Nest 2 repeatedly. One very pale individual, believed to have been a male despite its appearance, chased Sanderlings about, including the bird at Nest 2, and performed flight displays in full song. Nest 2 had a special attraction for it. At 17:22 on 9 July, Taylor saw the pale bird alight 10 feet from the nest, walk up, and circle it with scapulars and other feathers erected. The marked Sanderling leaped off the eggs, forced it back, and then chased it on the wing. After such a flight, the marked bird, obviously agitated, returned to the nest with feathers erected.

The pale Sanderling was a nuisance—and at times disturbing. At 18:30 on 9 July, it approached Nest 2 when the owner was off feeding and from 40 feet began chattering. Then it ran straight to the nest and began jabbing the eggs with its bill. Fortunately, not one egg was damaged. We saw this pale bird a few more times before it disappeared like those before it and other Sanderlings replaced it.

Sixteen times we recorded the arrival of small flocks — from two to seven birds — which, although they did not go directly to the nest, sometimes approached it closely. At most any distance the presence of a flock was too much for the incubating Sanderling. For example, at 05:14 on 11 July, MacDonald observed three Sanderlings drop down to the ground 150 feet from Nest 2. The marked bird flew off the eggs straight for them and, with wings and tail spread, landed among them, scattering all three. Then it pursued them on the wing, actually catching one in midair and landing squarely on its back. Four minutes later it returned to its eggs. Definitely an incubating Sanderling is hostile to strange Sanderlings. On the other hand, a freshly killed Sanderling specimen of either sex, propped with wires near Nest 8, incited no response whatever from the incubating bird, probably a male.

Although we were not absolutely sure that one of the many Sanderlings that came to Nest 2 was not the mate of our marked bird, we were certain that none of these birds actively took part in the incubation or brooding from 7 July onward. Conceivably the mates of incubating Sanderlings do visit the nest at times; clearly they play no real role. We can hardly accept Pedersen's belief (1942) that only the female Sanderling incubates, that the male Sanderling stays in the vicinity of the nest, meets her regularly when she goes for food, and, later, joins her and the brood in times of stress or emergency.

It soon became apparent to us that our marked bird was very much aware of strange birds and mammals that passed near or through its domain. In responding to all — predators or not — from buntings to caribou, it flattened out on the nest or ran quickly from the nest for a few to many feet and squatted low in a depression. Once the animal had passed through the area, the Sanderling quickly ran back to its eggs. Many times we first became aware of the presence of some bird or mammal by noting the behavior of the incubating Sanderling.

During long periods when it was incubating undisturbed, it held its head and neck upright and moved them back and forth often, turned about frequently, preened and arranged its feathers, moved the eggs, adjusted its brood patches and rearranged its feathers, picked at the saxifrage close by, and played with the lichens that lined the nest. It was quietest during the coolest hours and at such times usually appeared to sleep soundly, its head turned and bill tucked beneath the scapulars.

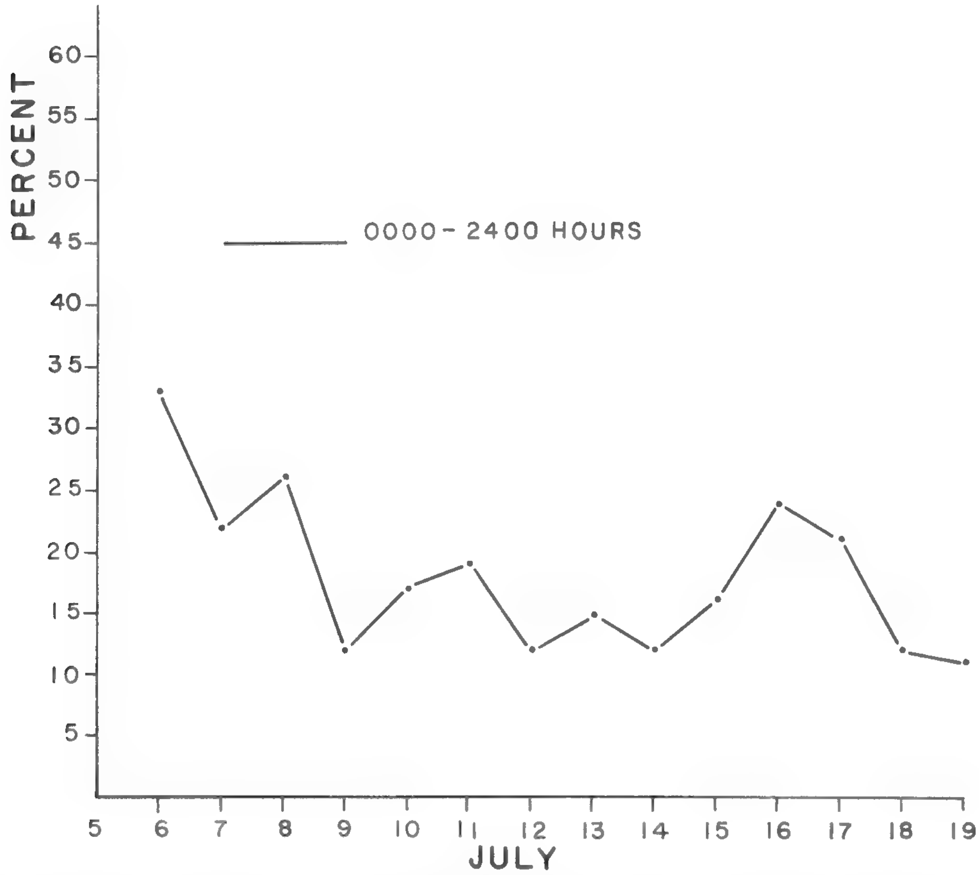

Figure 12. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during 00:00–24:00 hours for the period 6–19 July. This graph combines the data of Figures 10 and 11, and shows that the Sanderling spent 81 per cent of its time on the nest during two weeks in July.

Hatching

Although we did not determine precisely when each of the four eggs at Nest 2 became starred (developed cracks in shell), and later pipped (developed hole in shell), we recorded the times when we first observed the events. See Table 6.

From the data in Table 6 it is clear that almost five days (116.5 hours or more) may elapse from first indication of starring to hatching (Egg 2), or as little as two-and-one-half days (62.5 to 68.5 hours, Egg 4), even when allowing for an error of up to six hours; and that as many as 57.68 to 63.68 hours (Egg 1), or as few as 10.25 to 12.58 hours (Egg 3), may elapse from pipping to hatching.

At Nest 7, at least 84.25 hours elapsed between the first observed starring and the hatching of one egg; at Nest 8, at least 72.5 hours; at Nest 12, at least 110 hours. The interval from pipping to hatching was less than 24 hours for two eggs at Nest 13. Manniche's statement (1910) that the "bursting of the egg-shells will generally begin already some 3 days before the emergence of the young" is reasonable, but there appears to be much variation in the period between starring and hatching and between pipping and hatching.

Prior to hatching, the young Sanderling chips a circular path completely around the large end, or "cap," of the shell. At Nest 2, the parent flew off with the cap before the first chick had completely emerged from the remaining larger portion and it quickly flew off with the larger portion as soon as the chick was free of it. Exactly the same procedure took place with the second hatching—i.e., the parent flew off first with the cap while the chick was still in the larger portion of shell and later with the larger portion. The quick removal of the cap before the young emerged suggests that the parent may actually assist the chick in hatching, apparently the case with Stone Curlews (*Burhinus oedicnemus*) in the Old World (see Nethersole-Thompson, 1951:183).

TABLE 6

Timing of Events in Hatching of Eggs in Sanderling Nest 2

Egg number	*Starring first noted*	*Pipping first noted*	*Precise hatching time*	*Minimum time from starring to hatching*	*Minimum time from pipping to hatching*
1	15 July (18:00)	17 July (12:00)**	19 July (21:41)	99.68 hrs.	57.68 hrs.
2	14 July (13:00)	18 July (18:17)	19 July (09:30)	116.5 hrs.	15.21 hrs.
3	16 July (18:30)**	19 July (05:45)*	19 July (16:00)	69.5 hrs.	10.25 hrs.
4	16 July (18:30)**	17 July (12:00)**	19 July (09:00)	62.5 hrs.	45.0 hrs.

*Error less than 2.5 hours since the third egg was not pipped at 03:25 on 19 July.

**Error less than 6 hours since the third and fourth eggs were not starred at 12:33 on 16 July, and the first and fourth eggs not pipped at 06:10 on 17 July.

The third hatching at Nest 2 took place during a downpour and the parent did not remove the half shells immediately. When the rain abated some minutes later, it ran off with the cap, dropped it about 20 feet from the nest, ran back, grasped the larger portion, flew off, and dropped it a hundred yards or so from the nest. It removed the two parts of the shell during the fourth hatching as it had the first two. With the one exception, the bird dropped all the shell parts from 100 to 200 yards from the nest and immediately returned each time.

When the parent was purposely flushed from Nest 7 during a routine check, we discovered that it had been brooding a chick which, judging by the wetness of its down, was perhaps 15 minutes old. An empty eggshell lay beside the chick in addition to a pipped egg and two slightly older young. As sometimes happens, the cap of the empty shell was firmly attached to the larger portion. When the parent bird returned to the nest, it at once flew off with the two pieces, still attached, for a distance of 125 paces, alighted, dropped the whole shell on a bare spot of ground without any attempt at hiding it in one of many cracks in the turf, and returned to the nest in a flash.

TABLE 7

Spread of Hatching Time in Sanderling Nest 2

Young number	*Partial band number*	*Time of hatching on 19 July*	*Final departure from nest on 20 July*	*Age when nest abandoned*
1	125121	09:00	10:47	25.78 hrs.
2	125122	09:30	10:47	25.28 hrs.
3	125123	16:00	10:47	18.78 hrs.
4	125124	21:41	10:47	13.1 hrs.

The parent at Nest 8 was so obsessed with brooding its newly hatched chicks in a high wind that it never removed the last empty shell with cap still attached. Nor did it fly off with this shell that we later weighted down with a small stone and placed beside the nest. Evidently, Sanderlings are reluctant to remove shells during inclement weather. Probably they do not remove addled eggs at any time. Such an egg remained in Nest 12 when the young left.

Manniche (1910) mentioned the immediate removal of eggshells by female Sanderlings following emergence of the young but gave no details. All tundra sandpipers, noted by us over the years, usually removed empty shells from the nest immediately or soon after the young emerged—or as soon as they were aware of the empty shells. Pioneer studies by Nethersole-Thompson and Nethersole-Thompson (1942) showed that variation in eggshell removal occurs both intraspecifically and interspecifically in shorebirds; but there can be no doubt that a good many shorebirds remove the eggshells before the young leave the nest.

TABLE 8

Young Sanderlings Collected on Bathurst Island in 1968

*Specimen number**	*Date collected*	*Days of age*	*Sex*	*Weight†††*	*Wing chord†*	*Exposed culmen††*	*Tail†*	*Tarsus†*	*Remarks*
55561	20 July	2**	M	9.4		11.7		18.5	Yoke sac present
55562	28 July	2**	F	9.5		11.4		21.0	Yoke sac present; small stones and fragments of chitin in gizzard
55569	28 July	4 or 5**	F	13.3	23.0	13.3		20.5	
55570	28 July	4 or 5**	F	13.0	23.0	13.7		20.5	
55563	26 July	7***	M	17.1	31.0	14.3	0.0	20.0	
55571	3 Aug.	7**	?	17.4	30.0	14.7	0.0	20.0	With adult female
55572	3 Aug.	10-11**	M	27.4	57.0	14.7	8.0	21.5	With adult female
55573	4 Aug.	15***	M	39.7	84.0	19.0	17.5	23.5	
55575	8 Aug.	15**	M	39.1	83.5	19.1	20.0	24.0	With adult male
55574	7 Aug.	21-22**	F	56.1	107.0	21.5	34.0	25.0	Strong flying; with adult male

*Specimens in Canadian National Museum of Natural Sciences.

**Probable age.

***Known age.

†To nearest 0.5 millimeter.

†† To nearest 0.1 millimeter.

†††To nearest 0.1 gram.

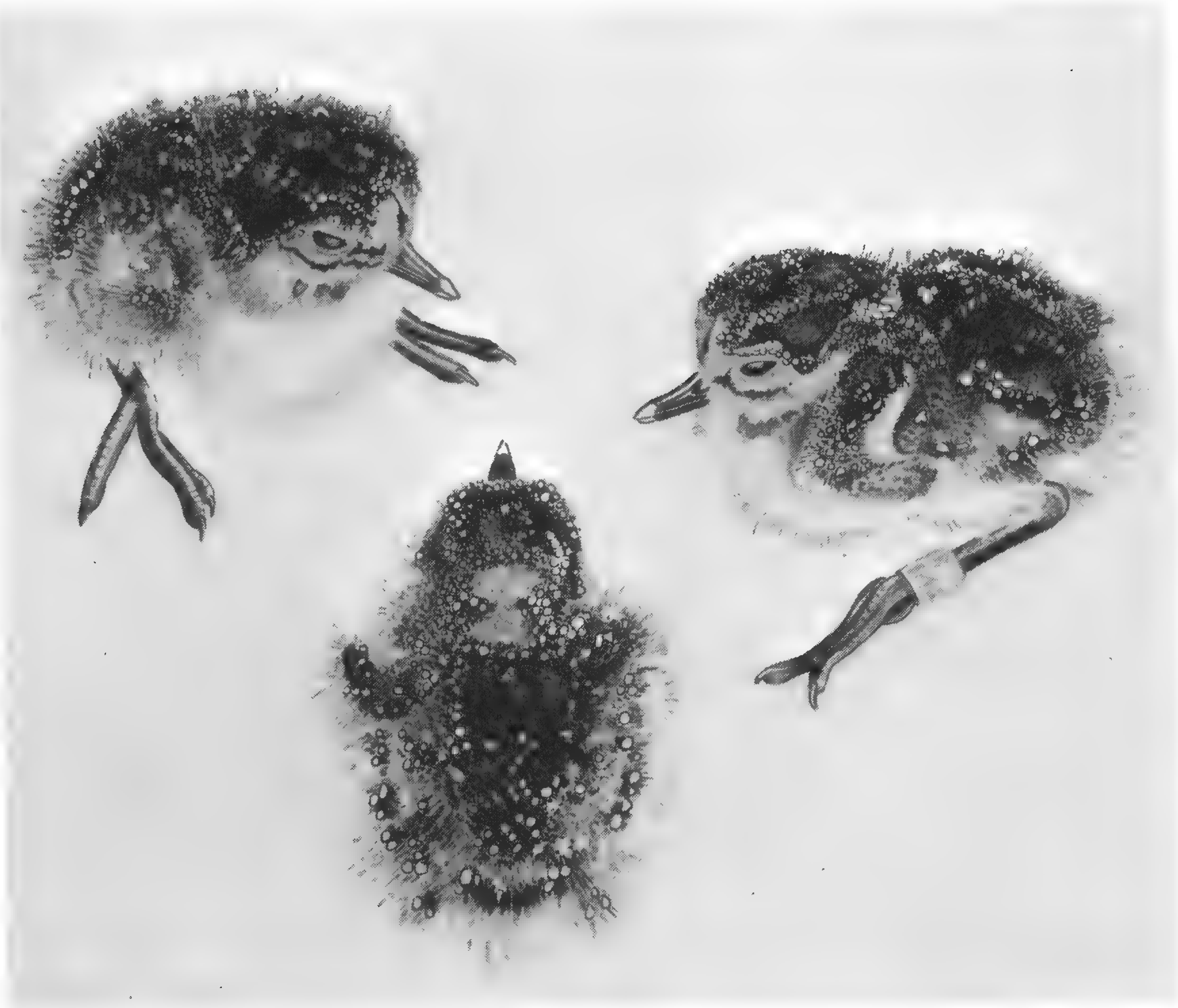

Figure 13. Fourteen-hour-old Sanderling. A chick in Nest 7 served as my model for this drawing. The chick hatched at about 04:00 hours on 24 July 1968 and was still in the nest at 18:00 when we made a detailed study of it. Juvenal plumage is not evident in a chick this age. Its eyes are black. The proximal two-thirds of its bill is dark gray or bluish gray, the distal third black except for the very tip and egg tooth. Legs and feet are black to bluish black with silvery highlights.

Since the chicks in one brood hatched at different times, they were obviously different ages when they left the nest together. The spread of hatching time was greatest in Nest 2 (12.6 hours); it was the least in Nest 11 (2.5 hours). See Table 7. At Nest 2, the only nest for which we have exact figures, the youngest chick was only 13.1 hours old when it faced the outside world. At Nest 8 we know that the youngest chick was not more than 13 hours old when it left – or was taken by a predator. The three chicks in Nest 12 probably hatched within an hour. All were wet when first seen. Since one egg in this nest was addled, we could not determine the hatching spread, nor did we know when the young left.

A Sanderling with wet down is a newly hatched chick. The down feathers dried and fluffed in a short time. Within 30 minutes the down of one was half dry; an hour later it was well fluffed though bits of membrane still adhered to the down. The fluffing of the down in other chicks took slightly longer. Figure 13 illustrates the fluffed-down pattern of a small chick.

Four newly hatched chicks at Nest 2 weighed 7.1, 7.5, 7.1, and 7.5 grams respectively. Attached to Chick 2 was an abnormally large egg sac that burst, spilling yoke onto the two pipped eggs. Later, the sac dried and the chick seemed none the worse.

Departure of Young from the Nest

Although we discontinued constant observations at Nest 2, following hatching of the last young on 19 July, I was in the blind and watched the final departure of the brood at precisely 10:47 on 20 July.

If one has any question as to whether the young Sanderling—or any other tundra sandpiper — ever returns to the nest once it departs, he can find the answer by spending some time near a nest. The young Sanderlings may run out of the nest and back to it many times, the more so as they gain in age and strength, and in time do so quite independently of the parent. However, the parent determines the final exodus and accomplishes this through persistent brooding at the nest followed by simulating feeding outside the nest.

Newly hatched chicks at Nest 2 were weak and almost helpless. Although capable of moving about in the nest, they remained mostly still, uttering low rasping *chucks*. Within an hour or so they were able to position themselves favorably beneath the adult. One chick, not more than 2.75 hours old, bounced outside the nest from beneath the parent and quickly crawled back. Either the first or second chick may have left the nest and ventured a few inches of its own volition when not more than three hours old, but it soon returned.

Except for these brief moments the young at Nest 2, as well as young at other nests, did not leave much before they were 12 hours old, though they were capable of doing so. They moved about freely in the nest, however, and on occasion climbed on top of the brooding parent, only to plunge and disappear again in the spread feathers of the brooding bird. Many times the brooding parent had difficulty in maintaining its balance when the brood moved about beneath it. Suddenly it rocked and wobbled, stood up with scapulars fully erect, turned about, hurriedly adjusted feathers, and plopped down on the squirming mass. When it flew off to feed, any chick less than 12 hours old stayed in the nest while older siblings ventured out and romped.

When 19 and 18.5 hours old, respectively, the two oldest young ran nimbly for 15 feet before returning to the nest. One or both left the nest 13 times during the four-hour period, 04:15–08:05, that followed, indicating that they were ready to leave the nest most any time even in the cool hours. Each of the 13 trips averaged a minute and did not exceed two. They ran about probing with their bills but soon became chilled. Twice they left, and four times they returned, when the parent was away. The rest of the time they left and returned when the parent was on the nest. The third and fourth young did not leave the nest once at this time.

During this four-hour period, the parent flew off to feed nine times for a total of 56 minutes — 24 per cent of the time. Each trip lasted five to eight minutes and averaged 5.6 minutes. The adult sometimes flew off even while its young were outside the nest. We noted the temporary abandonment of young by the parent at other Sanderling nests as well. For example, at Nest 8 on 16 July, while I lay on the ground only a few feet from the nest that held a chick and pipped eggs, the marked adult flew off to a distant marshy pond to feed four times in a 2.75-hour period. It stayed away for a total of 36 minutes (21 per cent of the observation period), each trip lasting five to 12 minutes and averaging nine minutes.

By 10:15 on 20 July, the morning of final departure from Nest 2, all four chicks were running hard. Now they all invariably ran from the nest when we purposely flushed the parent or when it flew off of its own accord to feed. They probed about, investigating everything they encountered. The oldest tested a purple saxifrage petal and swallowed plant bits. They became chilled after an expedition of two minutes and returned to the nest whether the adult was there or not. Twice the adult, on returning to an empty nest, waited for the chicks to run in, and this they most certainly did, one by one. Not once did the adult attempt to brood the chicks outside the nest.

At 10:47 the behavior of the brooding parent changed dramatically. Suddenly it called loudly from the nest. One chick ran off. Then the parent left and very deliberately walked about, jabbing the ground hard with its bill in simulating feeding. The effect was electrifying. The remaining three chicks bounded out of the nest and soon all four were scrambling behind the parent, probing as they went. At 10:49 two chicks, followed by the other two, ran to the adult. It brooded them where it stood, five feet from the nest, forever abandoned by the young.

Fledging Period

Following the final departure of the brood from Nest 2, we watched them for nearly two hours, 10:47–12:37. The parent bird repeatedly abandoned the young briefly and left to feed just as it had done many times previously when attending eggs or chicks in the nest. During the nearly two-hour watch, it was away for a total of 27 minutes (24 per cent of the observed time), each trip lasting two to nine minutes and averaging 6.7 minutes per trip.

The adult did not fly off each time it left the brood. More often it jumped away from the young and continued its probing action, though apparently it did not eat anything. The chicks exploded in all directions, fanning out within five feet of the adult and probing. After a few minutes the parent squatted and the chicks ran to be brooded. When the parent was away and they became chilled, they ran to one another and pressed close together, at times in pairs; at other times all four huddled in one downy bundle.

As mentioned previously, the parent brooded the chicks of Nest 2 five feet from the nest following the final departure. It brooded them again only four minutes later 10 feet from the nest. Gradually the distance between nest and brood increased until by the end of the first hour they had moved 60 feet, and by the end of the second hour, 210 feet.

We then discontinued observations until 00:30 the following day, 21 July, when the young were 26.81 to 39.5 hours old. They were probing for food in a favorite feeding area of the adult, a small creek bed kept wet by melting snow only 150 yards northeast of the nest. However, they had probably moved about considerably more since they initially traveled due south of the nest. All, appearing to be much stronger, ranged freely 15 feet from the adult before running back to be brooded.

Young Sanderlings sometimes travel long distances the first day out of the nest. Manniche (1910) actually observed young that had moved 500 to 600 meters hardly an hour after leaving the nest. Our evidence suggests that, as a rule, young Sanderlings and other young tundra sandpipers do not range far from the nest the first week of their lives. This was true of the brood from Nest 2. On 26 July, seven days after hatching, the marked parent tended three chicks in wet, hummocky tundra below a bank of snow only 553 paces from the nest. We collected one young (see Figure 14).

The good feeding areas close to Nest 2 may have kept the birds from moving far from the home ground. Unfortunately, we did not see them after 26 July, so we do not know whether they traveled to a new area or whether a predator found them.

That some Sanderling families move long distances from the nest was clearly evident when, at 22:10 hours on 3 August, Gray and Taylor caught and kept as a specimen one of the banded young from Nest 12 (see Figure 15). Almost 15 days old to the hour, not quite capable of sustained flight, and still with the marked parent, it had traveled fully two miles from a high, exceedingly barren slope to a lush, marshy valley. They saw no siblings.

An unbanded chick, collected on 8 August, was most likely the same age because it had nearly the same weight, measurements, and plumage development as the bird of known age (see Table 8). And like the latter, it could fly only a foot or two at a time just above the ground. The wing chords of both birds exceeded 80 mm (83.5–84.0) and no doubt were nearly long enough to support the birds in sustained flights for distances of 50 to 100 yards or more. White-rumped Sandpipers fly fairly strongly at 16 to 17 days of age when their

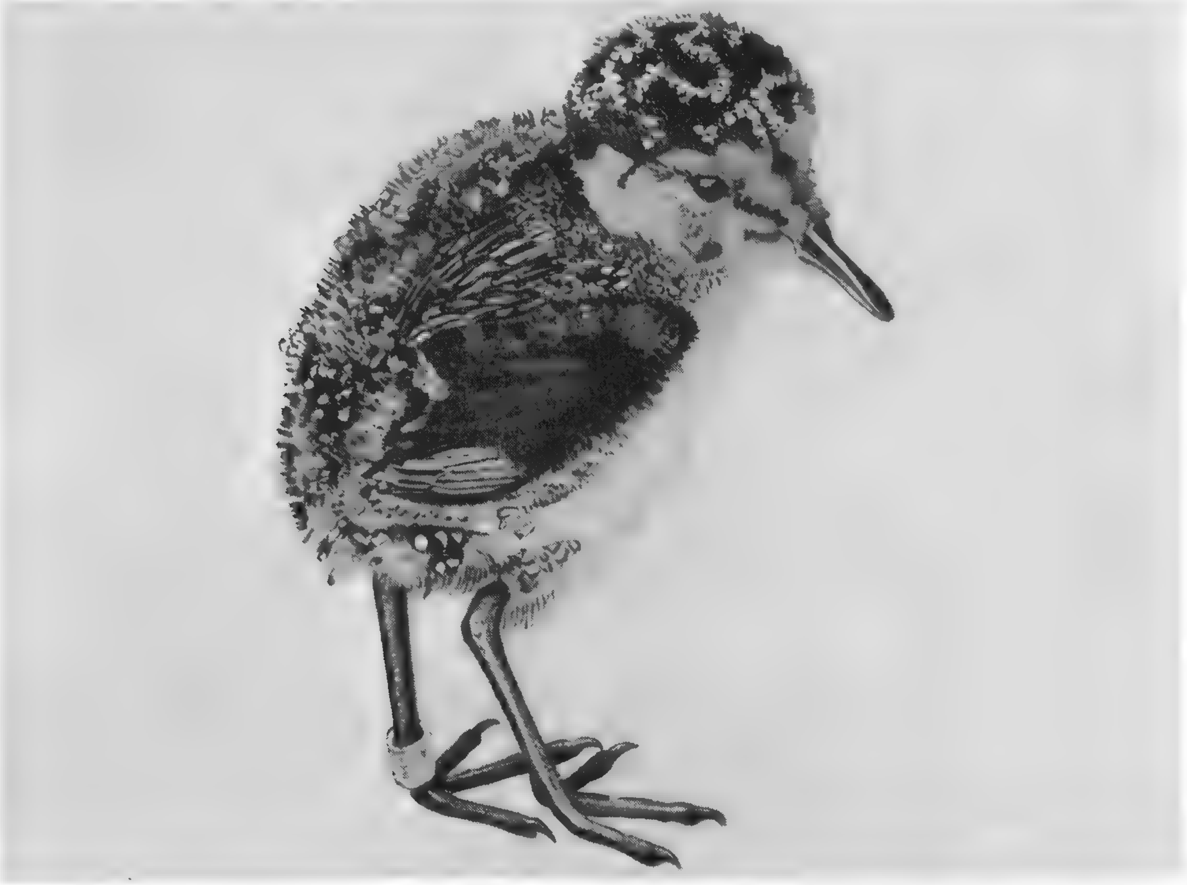

Figure 14. Seven-day-old Sanderling. I drew a chick that I had banded at Nest 2 on 19 July 1968 and found nearly seven days later with the parent and two siblings 553 paces from the abandoned nest. I returned to camp with the chick and preserved it at exactly seven days of age on 26 July. Although down is conspicuous on a chick this age, the juvenal plumage is developing rapidly above and below. The quills, about 13.0 mm, are starting to burst at the tips. Eyes, bill, legs, and feet are very dark, nearly black.

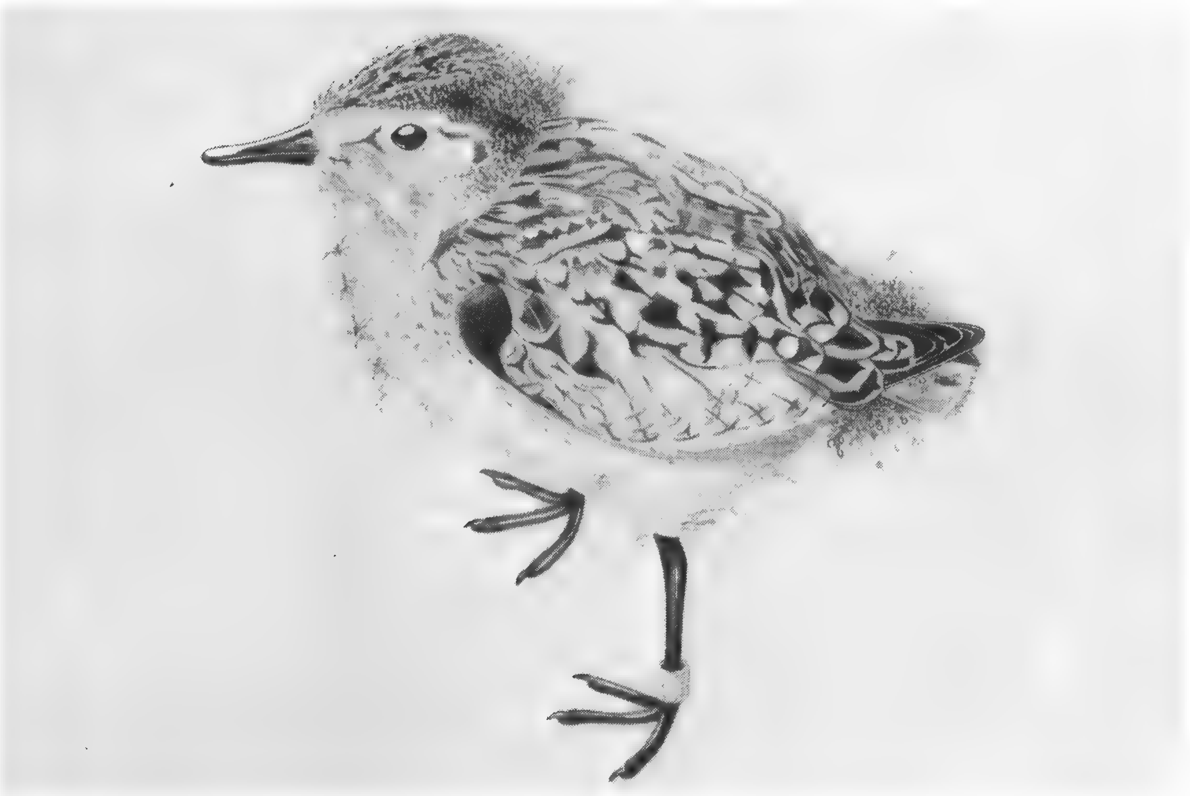

Figure 15. Fifteen-day-old Sanderling. I drew this illustration of a banded young caught on 3 August 1968 two miles from abandoned Nest 12. The drawing is also based on an unbanded young believed to have been 15 days old on 8 August. A Sanderling this age is not quite capable of sustained flight. Its juvenal plumage is conspicuous above and below. Down is still plentiful on parts of head, neck, mid-pectoral region, base of tail, and legs. Color of eyes, bill, legs, and feet is similar to that of seven-day-old.

chords exceed 80 mm (Parmelee *et al.*, 1968). However, Sanderling juveniles weigh considerably more than White-rumped Sandpipers of the same age and for this reason may require slightly longer wings before they become airborne. This aspect of fledging needs study.

If we use the criterion of sustained flight for a distance of at least 50 yards, the fledging period for the Sanderling probably averages close to 17 days. Certainly the "12 to 14"-day period, the so-called fledging period, given by Manniche (1910) and quoted by many authors thereafter, is too short.

Allowing 17 days from time of hatching to time of first sustained flight, we estimated that some young flew as early as 2 August on the Bathurst breeding ground in 1968. Most young probably flew by 2–9 August though a few, such as those from Nest 10 where laying was late, may not have flown much before 20 August.

On 7 August we shot one of two strongly flying juveniles and an adult male flying with and defending them at the time. This specimen was well developed (see Table 8) with wing chords 107 mm long. If we make a rough comparison between it and White-rumped Sandpipers of known age, the Sanderling was 22–23 days old.

Departure from Breeding Grounds

Other investigators in different places have noted the early flocking of Sanderlings on the breeding grounds. The flocks, made up of both bright and pale individuals, probably start forming in late June and become noticeable in early July and conspicuous by mid-July. According to Manniche (1910), the flocks are composed solely of males which have abandoned the females at the nest. Others have suggested that the flocks are composed not only of males but also of females which have lost eggs to predators. I believe that the flocks contain both sexes, non-breeding individuals and breeding individuals that have lost eggs.

The flocks seen on the Bathurst Island breeding ground usually numbered from four to six birds, and no flock exceeded 10 although larger flocks probably occur. We do not know when these birds left the area. It appeared that they flocked for some time before departing. In 1968 the flocks became scarce by late July and we saw no flocks anywhere from Bracebridge Inlet to Goodsir Inlet during 7–10 August when we noted only a few adults, all but one of which attended young well inland. We saw one lone adult a quarter mile from the beach of Goodsir Inlet on 10 August. In the southern part of the archipelago, I observed as many as 50 adults at one time on the beaches of Jenny Lind Island during 3–10 August 1966.

Autumnal departure dates for adult Sanderlings from the Canadian breeding grounds are scarcer than arrival dates because little attempt has been made to separate old birds from birds-of-the-year in the fall flocks. We have, however, no reason to doubt Snyder's conviction (1957) that the majority of adults leave by mid-August and a few linger with young birds well into September. Some of these unpredictable adults conceivably migrate south with young (see Sutton, 1932:149). In Greenland, where departures are well documented, the fall migration of adults takes place in late July and the first half of August (Salomonsen, 1950–1951).

Although we made a special effort to locate Sanderlings-of-the-year on the marine beaches of Bathurst Island in 1968, not a single young shorebird of any species did we find on the sandy beaches at the head of Bracebridge Inlet on 7 August, and only one — a lone Sanderling — on the beach at the head of Goodsir Inlet on 10 August. The paucity of young shorebirds clearly indicated a poor breeding season. Nevertheless, the Sanderling was one of very few bird species that produced even a few young that year.

Predation and Survival

We have no evidence of predation on adult Sanderlings. Presumably some losses occur although these quick, swift-flying birds are able to cope with most predators. They also are tough and well adapted to the Bathurst environment. We saw no signs of suffering among the early arrivals such as that described elsewhere. Pedersen (1942), for example, stated that Sanderlings suffered greatly from cold and scarcity of food immediately after arriving on the Greenland breeding ground. He reported birds sitting on the snow in small groups, obviously cold, although he found only a few dead.

For young Sanderlings in Greenland, which must have a remarkable survival rate some years, we have quite a different picture. According to Manniche (1910), the brood of the Sanderling seems to suffer very little from hostile persecution, a fact which may be due to the "accomplished vigilance and prudent behaviour of the old female and the young as well as the extremely suitably coloured clothing of these." Despite an abundance of predators, he did not find a single defective among "some 50 broods of downy young." Taken literally, every brood had four young!

Young Sanderlings on Bathurst Island did not fare so well. Of nine nests, not counting two collected, three were destroyed before hatching and one during hatching. Of a dozen broods seen out of the nest, nine were incomplete.

The Parasitic Jaeger and Long-tailed Jaeger (*Stercorarius parasiticus* and *S. longicaudus*) were the principal avian predators of Sanderling eggs and chicks in 1968. Both patrolled the breeding areas systematically. On 3 August, Taylor saw a Parasitic Jaeger catch a Sanderling chick. A few Glaucous Gulls (*Larus hyperboreus*) and Snowy Owls (*Nyctea scandiaca*) also hunted throughout the Goodsir-Bracebridge area. We do not know what effect these birds and the much rarer Gyrfalcon (*Falco rusticolus*) had on the Sanderling population.

The following mammals occurred in the Sanderling nesting areas and, though we have no direct evidence, may have been potential predators. The arctic fox (*Alopex lagopus*) was fairly abundant and probably the principal mammalian predator on birds in 1968. Wolves (*Canis lupus*), which occasionally investigated our observation blind, came dangerously close to Nest 2. Though not predatory in the usual sense, caribou (*Rangifer rangifer*), musk-oxen (*Ovibos moschatus*), and particularly arctic hares (*Lepus arcticus*) frequented the Sanderling ridges and could have stepped on a few nests accidentally. Nest 2 had its closest call when a baby hare ran over the eggs and dented one with its toenails.

On the approach of a bird or mammal, the incubating Sanderling either crouches or runs from its eggs and squats some distance away – a behavior seen a number of times from the blind at Nest 2. Since a man's relatively slow approach gives ample warning, very likely the Sanderling leaves its eggs long before the man is close to the nest. At least it leaves the first time or until it becomes accustomed to such approaches. The fact that the Sanderling usually runs from the eggs at the approach of danger explains why Sanderling nests are difficult to find and has led some investigators to believe that the Sanderling does not engage in the "rodent-run" and "injury-feigning." The truth is that the incubating Sanderling, at the approach of a man, may occasionally leave the nest at the last moment and creep away like a lemming; or it may beat its wing furiously on the ground, partially or fully spreading its down-turned tail, and scuttle and drag itself over turf and bare ground, crying pitifully as it goes – reminding one of a Knot that has just left its eggs.

We found Nest 9 by first seeing the incubating bird feigning injury a long way from the nest and then watching it run back to the eggs. Although we visited Nest 9 rather frequently and often watched the site from afar, the marked adult always ran from the eggs before we were close enough to see it leave. However, this bird quickly returned to the nest. Other Sanderlings, once their nest was discovered, behaved differently. They, like the adult of Nest 2, often could be approached closely and photographed from only inches away. Nevertheless, we knew they were under stress by their involuntary trembling. Even the highly conditioned adult of Nest 2 trembled some when we were too close.

A distress call, often repeated, was sometimes given near the nest by adult females.

The facts that the Sanderling is inclined to run from the nest in the presence of danger, and that it leaves both eggs and young during routine feeding excursions, point up the importance of cryptic coloration in eggs and young of the species. One seemingly serious flaw in the Sanderling's behavior, first noted at Nest 2, is that Sanderling chicks move about conspicuously in and out of the nest while the parent is away feeding, which is about 19 per cent or more of the time. When running about unattended, they are conspicuous to the human eye and, we have reason to believe, particularly vulnerable to predators.

When the adult is on hand and danger approaches, it gives a sharp *wheat* or rapid *wit-wit-wit,* either of which stops the chicks at least momentarily. We first heard these quieting notes at Nest 2. There the adult began calling *wheat* or *wit* before the young hatched. Seemingly, the peeping of the chicks within the shells stimulated the parent. Unfortunately, we did not record these calls.

The adult attending the brood is highly solicitous of the chicks and defends them by attempting to lead potential enemies away. The quieting notes are a dead giveaway that chicks are in the vicinity. Locating Sanderling chicks is easy because the parent is prone to return quickly to them, even more quickly than to the eggs.

In addition to predators, the temperature in the Arctic subjects the Sanderling chicks to considerable stress. They are highly sensitive to cold and die quickly if not brooded regularly at short intervals. Although we did not determine the lethal limits of exposure, we do know that, after two minutes in temperatures approaching freezing, a small chick is under great stress and, after 15 minutes, it is so numb and stiff that it barely can move its legs. Two chicks, carried in a telescope case by Manniche (1910), were "both lying dying in convulsions" after 15 minutes of exposure. No one has yet determined the age when a young Sanderling is able to withstand cold.

The brooding Sanderling, which may occasionally abandon its eggs for unbelievably long periods, will remain with the chicks under adverse conditions — a behavior also noted by Manniche (1910). This certainly was the case following hatching of the first two chicks at Nest 2 on 19 July. Rain fell unusually hard that day and drenched the parent bird attempting to shield both eggs and young. So wet was the bird that it at times stood up and shook its body feathers violently, sending sprays of water out in all directions. Then it settled down and very deliberately stripped the remaining water from each primary with its bill. Once during a severe downpour it did not leave the nest even to carry off the shells of a newly hatched chick.

Banding Returns

To date we have had three recoveries of Sanderlings, banded on the Bathurst breeding ground. An adult male, banded at Nest 5 on 2 July 1968, was collected at Nest 14 on 28 June 1969. The two nests of different years were only 110 paces apart. Collecting the bird verified the sex, which we thought was a male from the start of observations at Nest 5.

An adult male, banded at Nest 7 on 16 July 1968, was trapped and then released at Nest 13 on 6 July 1969. The two nests of different years were fully two miles apart on ridges separated by a broad valley. We verified the sex of this bird in 1969 when we observed its unbanded mate laying eggs and we saw him on 31 July 1969 with his young at Nest 13.

A bird-of-the-year, banded when newly hatched at Nest 11 on 20 July 1968, was shot in the Gulf of St. Lawrence at Dune du Sud, Magdalen Islands, Quebec, on 20 October 1968. This recovery is important because it indicates that Bathurst Island Sanderlings, unlike the Knots of this area, migrate south to the New World rather than to Old World wintering grounds. J. Claude Baudreau made the recovery.

Specimens of Young Sanderlings

The probable age, weights, and measurements of 10 young, collected on Bathurst Island in 1968, are given in Table 8. A description of body-plumage development and colors of soft parts is outlined below:

Probable Two to Five-day-old Young

Down conspicuous everywhere; feather sheaths of juvenal plumage appearing on interscapular, humeral, dorsal, sternal, and axillar regions of two larger chicks.

Soft parts: eyes black; proximal two-thirds of bill dark gray or bluish gray, distal third black except for small whitish tip; legs and feet black to bluish black with silvery highlights.

Seven-day-old Young

Down conspicuous. Juvenal plumage inconspicuous but developing rapidly: sheaths well developed and bursting at tips on interscapular, humeral, and dorsal regions; sheaths well developed on lower cervical, sternal, and axillar regions. Quills, about 13.0 mm, starting to burst at tips. Wing chord length and juvenal plumage development similar to those of a White-rumped Sandpiper, six and one-half days old, except that the sheaths on the dorsum of the White-rump were not bursting noticeably.

Soft parts: eyes black; bill dark gray to nearly black, being darkest at tip except for trace of whitish; legs and feet very dark greenish gray to black.

Probable 10 to 11-day-old Young

Down about as conspicuous as juvenal plumage, especially noticeable on head, neck, midventral, upper wing, rump, and thigh regions. Feathers conspicuous only on coronal and auricular regions of head, but well developed and fluffed on interscapular, humeral, and dorsal tracts above and on lower cervical, sternal, axillar, and abdominal regions below. Crural regions mostly downy with incoming juvenal feathers apparent. Remiges, including wing-bars, obvious. Compared well to White-rumped Sandpiper of known age.

Fifteen-day-old Young

Down less conspicuous than juvenal plumage but still plentiful on head (except on coronal and auricular regions), neck, mid-pectoral region, base of tail (pelvic and abdominal regions), and legs (crural region). Juvenal plumage conspicuous above and below; the grayish buff of lower throat, pectoral region, and along sides of body distinct from white belly. Wing chord length and juvenal plumage development similar to that of a White-rumped Sandpiper, 15 and one-half days old, except that more down showed on the Sanderling's head.

Soft parts: similar to those of seven-day-old, at most a shade or so lighter.

Probable 20 to 21-day-old Young

Down still conspicuous at base of bill, throat, above and behind eyes, neck, above and below base of tail, and on thighs; traces on pectoral region; otherwise juvenal plumage highly developed and conspicuous. Compared well to White-rumped Sandpiper of known age.

Conclusion

The Arctic summer is brief for man as well as birds and the pressure to see and record every action tremendous. In working over the notes and summarizing the material amassed by the members of the 1968 and 1969 expeditions, I realize that we added a lot of information on the mating and nesting behavior of Sanderlings. The chance to follow one nest from the laying of the eggs to the successful departure of the brood was an opportunity not even anticipated. I am also aware that there are many gaps – phases of the life history that we neglected or could not observe. However, the details that we now have on pairing, mating, and nesting should make future work on this species easier and the prospects of additional studies more appealing, especially since the Sanderling appears to have one of the most complex breeding behaviors of any scolopacid studied to date.

Summary

This paper describes a study of the Sanderling (*Crocethia alba*) conducted on Bathurst Island near the 76th parallel in the Canadian Arctic during the summers of 1968 and 1969. It emphasizes courtship and mating activities, pair-bond relationship, and the role of the sexes in the care of the eggs and young. Working inland, between Goodsir and Bracebridge Inlets, where dry and wet habitats are extensive and suitable, we made observations on 14 nests, one of which we kept under constant surveillance for 14 days. We also banded and color-marked nine birds with eggs or broods and banded 23 young of known age and 15 of uncertain age.

The Sanderling pairs were thinly scattered, not more than six or eight pairs to one square mile in 1968 and much less in 1969, even on the choicest nest ground.

Both sexes arrived together in small flocks between 3–9 June 1968 and 8–15 June 1969. Some appeared paired on arrival; others loafed and fed in pairs soon after; few appeared to be unmated. We observed single males advertising for mates and defending territories, flight chases, flight displays, and ground displays.

Sanderlings use precopulatory scrapes apart from nesting scrapes for mating purposes. A description is included.

Nests were slight hollows containing dry leaves and lichens. With one exception, the clutches had four eggs. Eggs were laid at intervals of 26 to 29 hours. The incubation period for two nests varied: 24.2 days in one, 31.6 days in the other. The pair-bond dissolves before incubation begins and only one adult, either male or female, incubates the eggs and attends the young.

The details of the activities and behavior of a nesting Sanderling are based primarily on a round-the-clock observation of over 14 days and include times on and off the nest, reactions to the observers, mammals, and other birds, hatching and behavior of the brood, and the final departure from the nest.

The period from hatching to first sustained flight was close to 17 days and an adult defended one strong flying young for five or more days longer. Most Sanderlings probably flew strongly for the first time during 2–9 August.

Flocks, composed of adults of both sexes, occurred in early July, were conspicuous in mid-July, and diminished in late July.

Adult Sanderlings resisted predation, weather, and lack of food; eggs and young were victims principally of jaegers and probably foxes.

Recoveries in 1969 of Sanderlings, banded in 1968, showed that at least some males return to the same breeding grounds and nest close to or far from the former nest. The recovery of a banded bird of the year in the Gulf of St. Lawrence indicated that Bathurst Island Sanderlings migrate south in the New World.

The weights, measurements, and a brief description of plumage development and colors of soft parts are given for 10 young collected in 1968.

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THE SCARLET IBIS IN SURINAM AND TRINIDAD

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The Scarlet Ibis (*Eudocimus ruber*), for all its striking color, large size, and colonial nature, is not a well known bird. The references in the literature are sparse. Even the fullest account by Penard (1926) consists mainly of secondhand reports garnered from hunters and fishermen. More recently Zahl (1950, 1954), Saunders (1956), and Lindblad (1969) have given us popular accounts; and De Vries (1966) and Haverschmidt (1967) commented on the existence of colonies in Surinam. Palmer, in the North American Handbook (1962) had little to say, indicating how very little we know about this extraordinarily beautiful creature.

We, Haverschmidt working in Surinam from 1946 to 1968 and ffrench in Trinidad from 1956 to 1969, made separate, but parallel, studies of the Scarlet Ibis, concentrating on the birds mostly during the breeding season. Haverschmidt dealt mostly with a colony near Gandoe, Surinam; ffrench studied a population in the Caroni Swamp in Trinidad (Figure 1), visiting this location 44 times from 1963 to 1966, and on 40 occasions during the other years. Because the Scarlet Ibis commonly inhabits desolate mangrove swamps on the sea coast, we were continually at the mercy of the tides that hampered our movements and limited our observations.

General Distribution

The Scarlet Ibis is confined to the northern part of South America — Colombia, Venezuela, Trinidad, the Guianas, and northeastern Brazil (Meyer de Schauensee, 1966). Vagrants show up fairly often on the islands of Tobago and Grenada, and there are a few isolated records from Central America and southern United States. While we know of some breeding localities in Venezuela, Surinam, and Trinidad, clearly we are unaware of a number of others partly because few observers venture into the wild country that Scarlet Ibises prefer.

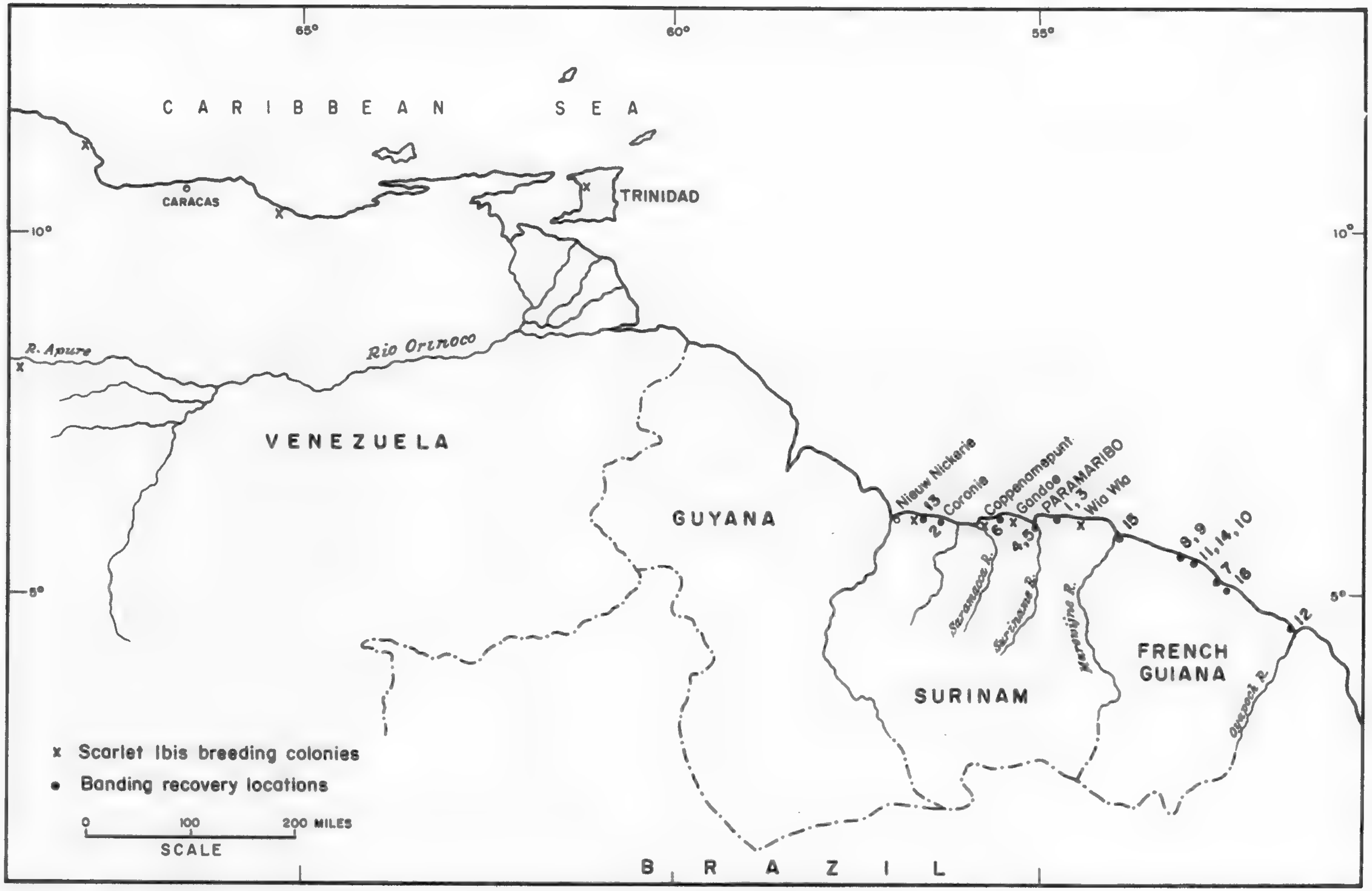


Figure 1. Map showing the sites (X) of Scarlet Ibis colonies studied in Trinidad and Surinam, and the localities (numbered) where ibises banded in the colonies have been recovered.

Colony Sites and Habitat

Although most of the breeding colonies of the Scarlet Ibis are in swamps along the seacoast — as were those we studied, this is not always true. Zahl (1950), in September 1949, found a large breeding colony in Venezuela between the Rios Apure and Matillure, hundreds of miles from the coast. This is the only sizeable inland colony we are aware of. In Guyana, the Scarlet Ibis occurs most commonly in the west near the Wainie River (Snyder, 1966), but no one has recorded it breeding there in the last ten years (Lindblad, 1969). According to reports, the same holds true for French Guiana and northern Brazil although the bird probably breeds there in areas yet to be discovered.

Status and Habitat of the Scarlet Ibis in Surinam and Trinidad

In Surinam the Scarlet Ibis inhabits the coastal mud flats and forests of mangrove (*Avicennia nitida*), venturing up the rivers and into inland mangrove forest only in times of drought. Normally it remains along the coast throughout the year.

We know of four distinct breeding colonies in Surinam in recent years, three of them operating simultaneously (Figure 1). The western colony between Nieuw Nickerie and Coronie was active in 1953 and 1966, that at Coppenamepunt in 1947, 1948, 1952, 1964, and 1965. The Gandoe colony (Figure 2) flourished in 1966 and 1967, when ibises deserted the Coppenamepunt locality, but was not used in 1968 or 1969. Scarlet Ibises were active in an eastern, and somewhat inaccessible, colony near Wia Wia in 1966 and 1967.

In Trinidad the Scarlet Ibis similarly confines its activities mainly to coastal mangrove swamps, in particular the Caroni Swamp (Figure 3). Smaller populations dwell in the mangrove swamps of Oropouche, Rousillac, and Los Blanquisales; but one rarely sees an ibis in the Nariva Swamp, a largely freshwater area with a negligible mangrove belt.

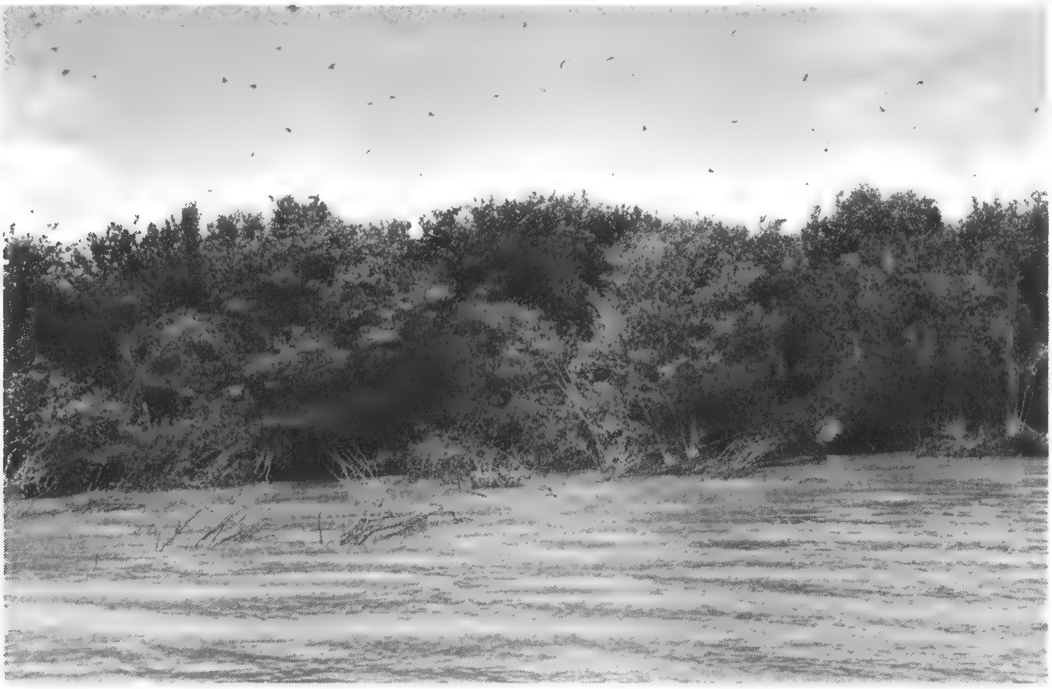


Figure 2. The nesting colony near Gandoe, Surinam seen from the sea at high tide. The birds nest in the low mangroves (*Avicennia nitida*), often just above the level of the high tide. Photograph by F. Haverschmidt.

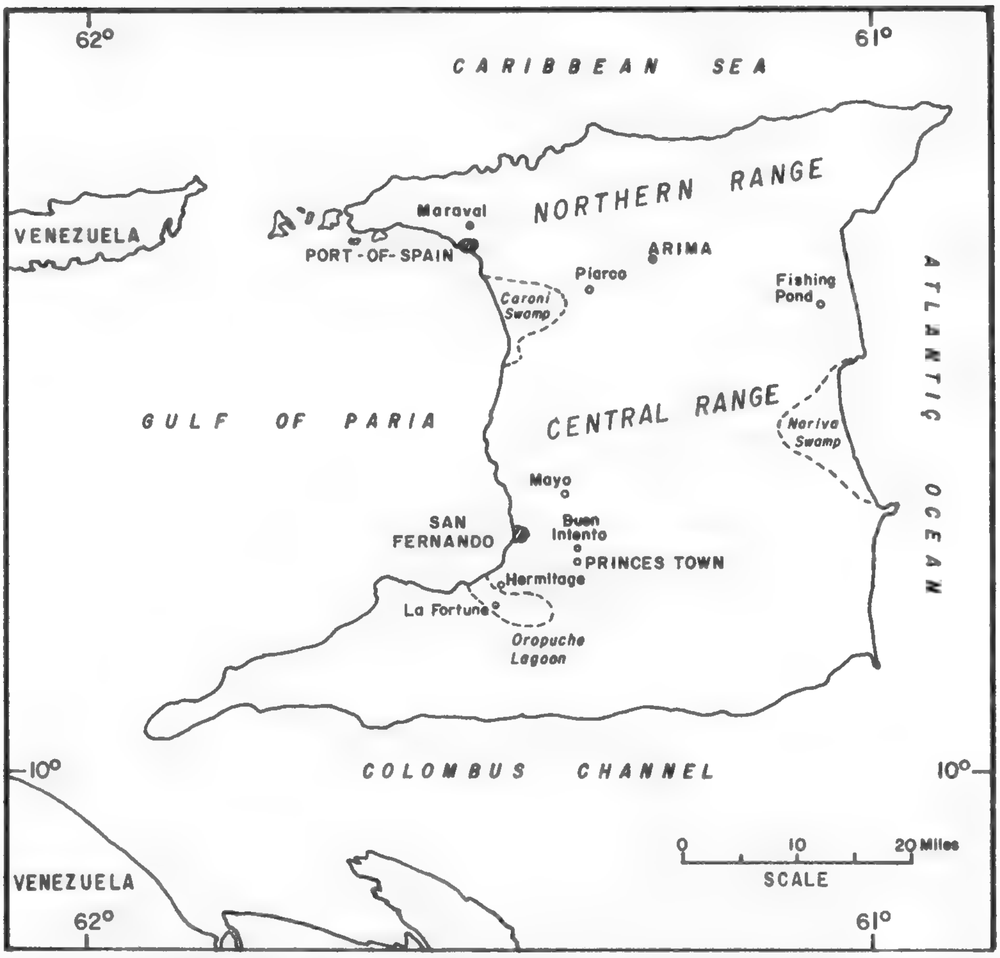


Figure 3. Map showing the location and the extent of the Caroni Swamp, the major breeding area for Scarlet Ibises in Trinidad. While no colony has been discovered in the Oropouche Swamp, about one thousand adults frequent the area, and some movement occurs between the two areas.

In the Caroni Swamp the population seems well established and breeds almost every year. Since 1953, when the government finally provided adequate protection for the Scarlet Ibises, they have nested there every year except 1964 and 1968. The adult population averages about 5,000 birds, diminishing from October to March when some birds depart, probably to Venezuela. Perhaps 1,000 adults frequent the Oropouche Swamp; while we suspect that they breed there, we have no proof. Certainly, the ibises move to some extent between the Caroni and Oropouche Swamps.

Associated Species

In both Trinidad and Surinam the Scarlet Ibis nests and roosts in company with herons, especially the Little Blue Heron (*Florida caerulea*), the Tricolored Heron (*Hydranassa tricolor*), and the Snowy Egret (*Egretta thula*). In addition, smaller numbers of Common Egrets (*Casmerodius alba*), Yellow-crowned Night Herons (*Nyctanassa violacea*), Black-crowned Night Herons (*Nycticorax nycticorax*), and Boat-billed Herons (*Cochlearius cochlearius*) associate with ibis colonies. In Trinidad, the Cattle Egret (*Bubulcus ibis*), having increased rapidly since its arrival in 1951, now probably associates with the Scarlet Ibis at the roost in greater numbers than any other heron. Only a few Cattle Egrets, however, nested in the Surinam colonies, along with some White-necked Herons (*Ardea cocoi*) and Roseate Spoonbills (*Ajaia ajaja*) (Haverschmidt, 1968).

Predation

The Scarlet Ibis appears to have few natural enemies in the mangrove swamps. In Trinidad the water rat (*Nectomys squamipes*) takes uncovered eggs. The Greater Ani (*Crotophaga major*) also takes heron's eggs. In Surinam the Long-winged Harrier (*Circus buffoni*) does the same. The scavenging Yellow-headed Caracara (*Milvago chimachima*) appears regularly in Surinam mangroves and may rob nests although we have not observed it. We have often seen Black Vultures (*Coragyps atratus*), Turkey Vultures (*Cathartes aura*), and even Magnificent Frigate-birds (*Fregata magnificens*) sailing high overhead, but they apparently take only dead nestlings that have fallen from nests.

Other possible predators include the crab-eating raccoon (*Procyon cancrivorus*), crabs, and snakes. Without a doubt the most serious predator is man. Fortunately, now both Surinam and Trinidad have established sanctuaries to protect the breeding birds and passed laws forbidding the hunting of the Scarlet Ibis.

Food

In Surinam the Scarlet Ibis feeds mainly on small crabs and molluscs including the gastropod *Melampus coffeus* and bivalves. In Trinidad the prey is principally fiddler crabs (*Uca* spp., especially *U. rapax* and *U. thayeri*).

The Scarlet Ibis catches a fiddler crab by probing in mud, often deeply, to the base of the bill. The bird brings up its prey in the tip, works it gradually up between the mandibles, and swallows it. Larger prey the bird frequently dismembers, sometimes washing the pieces in a puddle before swallowing them. Usually it discards the large claw of the bigger crabs. Our observations of Scarlet Ibises feeding in different situations indicated that they are more successful in obtaining prey when feeding in shallow water than on exposed mud.

An analysis of the stomach contents of Scarlet Ibises shows that, in Surinam, they also feed on insects, including the larvae of Diptera (Stratiomyidae), shield-bugs (Pentatomidae, including *Edessa* sp., and Naucoridae), and water-beetles (Hydrophilidae). Some fish, including Characidinidae (*Erythrinus erythrinus*) and Cichlidae, comprise part of the diet. In Trinidad, they take small fish and snails, and small amounts of green algae have been found in the stomach.

In Trinidad, adult birds, while ordinarily foraging in saltwater or brackish-water swamps, frequently move to freshwater marshes, rice fields, and flooded savannas when feeding young in the nest. At this time their diet may well consist more of insects and small amphibians, but we have too few data to confirm this.

Breeding Biology

The Breeding Season

According to local belief, the Scarlet Ibis begins to breed soon after the onset of heavy rains, which in Surinam occur in mid-April, and in Trinidad in late May. In neighboring Guyana, Lowe-McConnell (1967) found this same response to the wet season to be true of some species of herons.

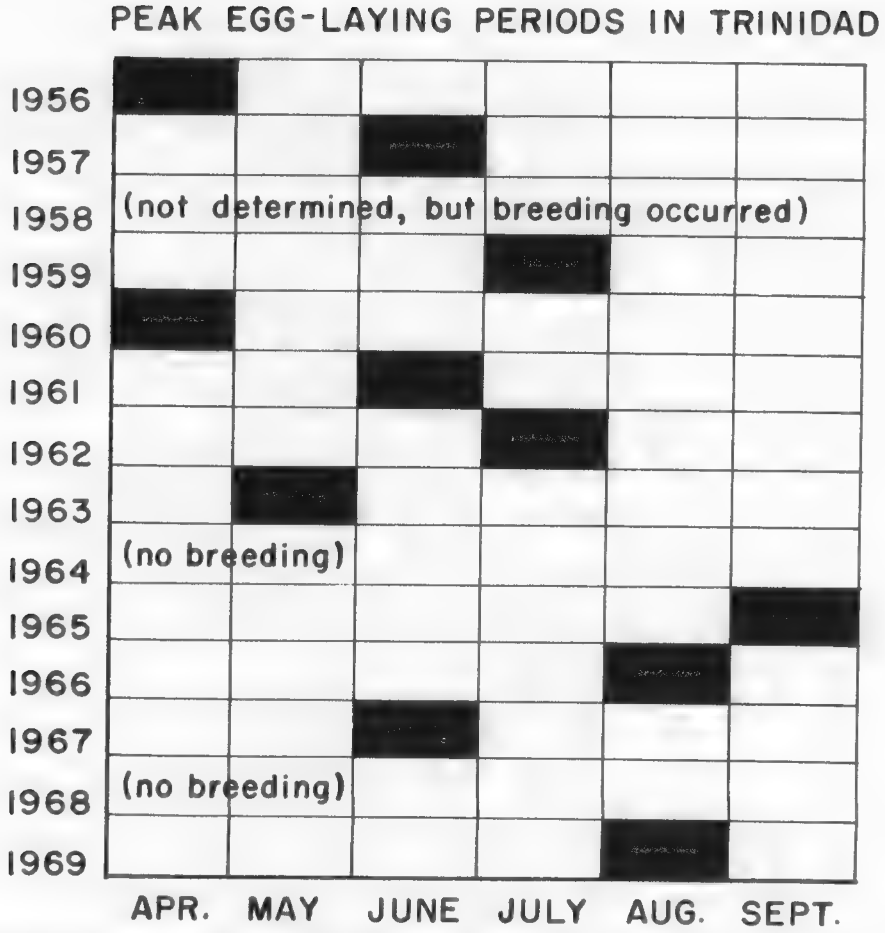


Figure 4. During the fourteen-year period 1956 to 1969, the Scarlet Ibises nested at a different site within the Caroni Swamp each year and also at a different time. The peak month of egg-laying varied from year to year by two months between April and September.

Breeding records of the Scarlet Ibis in Surinam support this view except that throughout the whole rainy season ibises are continually settling down and starting nests. In any one colony at any one time an observer may find nests with fresh eggs and young birds already flying. At Gandoe, in 1967, where a few pairs of ibises had nests with eggs as early as 23 April, there were many nests with eggs on 27 August and a few as late as 24 September.

In Trinidad, Scarlet Ibises maintain a loose temporal cycle, coordinating their breeding to the wet season, normally May to November. Figure 4 shows the peak months for egg-laying. These data do not support the theory that climatic changes trigger the onset of breeding. However, certain factors, such as disturbance by man (tourist, fisherman, or poacher), pollution of parts of the swamp by poisonous effluents from nearby factories, or even competition for nest sites with other species such as the Cattle Egret, may possibly alter or inhibit the beginning of breeding. Some factor or factors affected the breeding cycle in Trinidad in 1964 and 1968, and no nesting occurred.

Compared to the herons, the Scarlet Ibis is nervous and wary. It is much less tolerant of man, so much so that human disturbance at a critical moment in the cycle may prevent the birds breeding that season. The failure of the birds to breed in the Caroni Swamp in 1964 and 1968 may have been due to a shift of part of the population to Venezuela during those years. Many immature birds appeared in the Caroni Swamp in July and August 1964. There were so many more than occurred when the birds bred locally that ffrench felt they must have come from the mainland of South America.

The Shifting of the Breeding Site

One aspect of breeding which at present defies explanation is the tendency of Scarlet Ibises to shift their nesting area from year to year, sometimes only a few hundred yards, occasionally several miles.

In Surinam the existence of the colony at Coppenamepunt for several years up to 1965 and its abandonment in 1966 and 1967, coupled with the appearance of a new colony at Gandoe those last two years, leads us to believe that the Coppenamepunt birds moved to Gandoe, a distance of forty miles.

Close study of the Caroni colony in Trinidad over most of the years 1954–1967 shows that rarely does the Scarlet Ibis nest in exactly the same patch of mangroves in consecutive years. Saunders (1956) found that, soon after the Caroni colony had been established, slightly differing localities were used for breeding from 1954–1956. In the ten breeding sites, recorded during the years 1957–1967, Scarlet Ibises used at least five other sites. Red mangrove (*Rhizophora* sp.) predominated at all the sites, and no one site appeared to have any topographical advantage over the others.

In the later years of this study, especially 1966, the ibises in Trinidad seemed to select for breeding an area already in use by nesting herons, especially the Cattle Egret, although in 1960 the ibises bred earlier than the Cattle Egret.

The Nest Site and Nests

When not breeding, Scarlet Ibises leave the roosts in the morning and return late in the day. The presence of large numbers of birds in a certain area throughout the day indicates that the birds have selected that area for nesting, and breeding will begin soon. At first, except for increasing aggressiveness toward rivals and trespassers, the birds show little activity. After a few days at the site, they start building their nests.

In Surinam the Scarlet Ibis nests low, seldom more than five feet above the high-water mark, in the black mangrove (*Avicennia nitida*), never in the tall *Avicennia* trees. In contrast, ibises in Trinidad build their nests much higher. In the spindly *Avicennia* or the white mangrove (*Laguncularia*) the nests are frequently about 15, or even up to 35, feet above high water. In the robust spreading red mangrove, they may be from eight to 40 feet above high water, the variation in elevation depending entirely on the location and shape of the branches. Of the very few nests below eight feet, two were on the ground, one on a ground level root. These ground nests were fairly substantial, one or more feet deep with the high-tide mark near the top of the nest. The young birds in these ground nests looked stunted.

Ibises construct their nests in the forks of branches or where two branches cross (Figures 5 and 6). They interweave mangrove twigs, mostly dry and a few green with leaves, in and around the supporting branches. Since they place dry twigs in the base of the nest and those with fresh leaves in the upper part, the green leaves, though they soon wither, last long enough to enable one to differentiate between old nests and newly constructed ones. The nests measure about 12 inches across; the twigs making up the framework measure about nine inches. Nests constructed where two branches cross often disappear in bad weather. All are fairly flimsy, yet rarely thin enough to see through and the

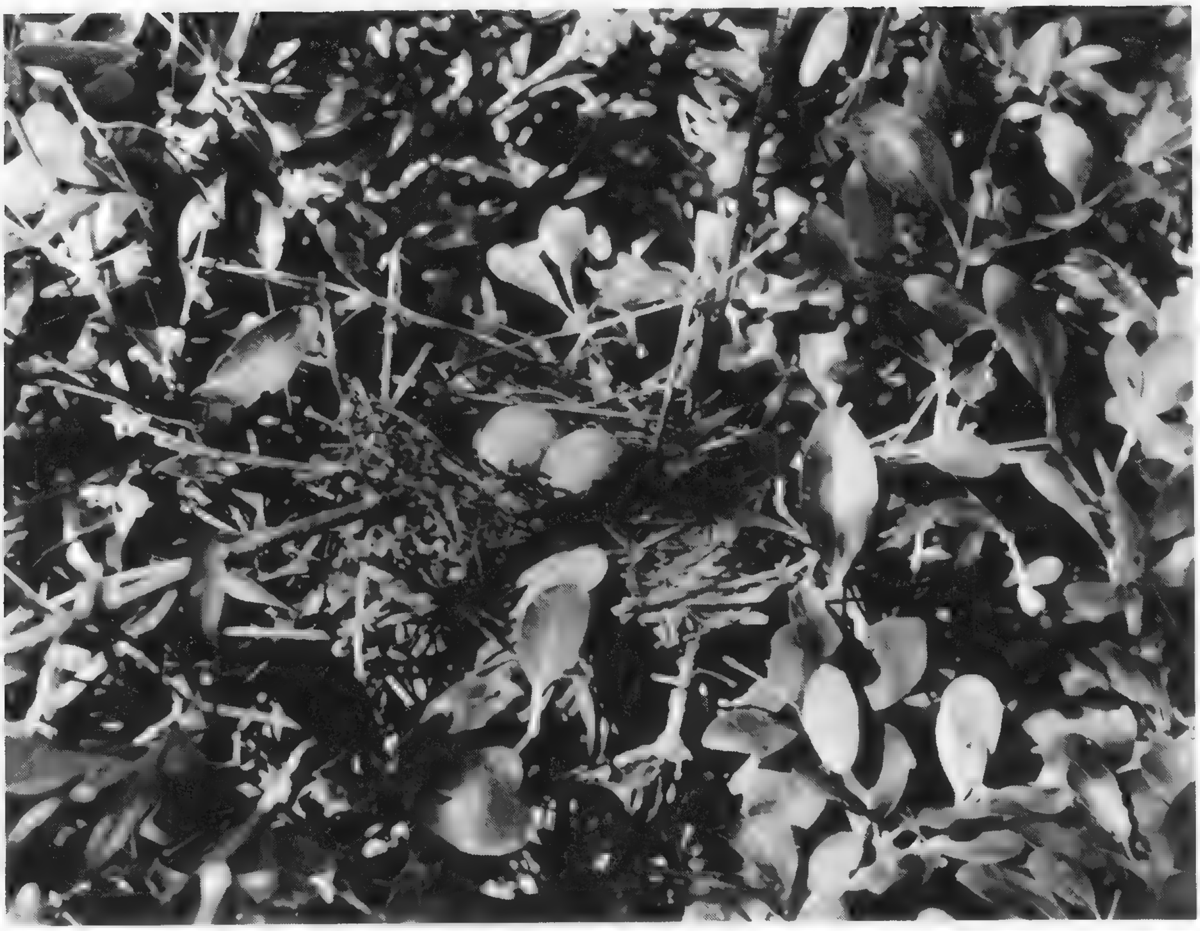
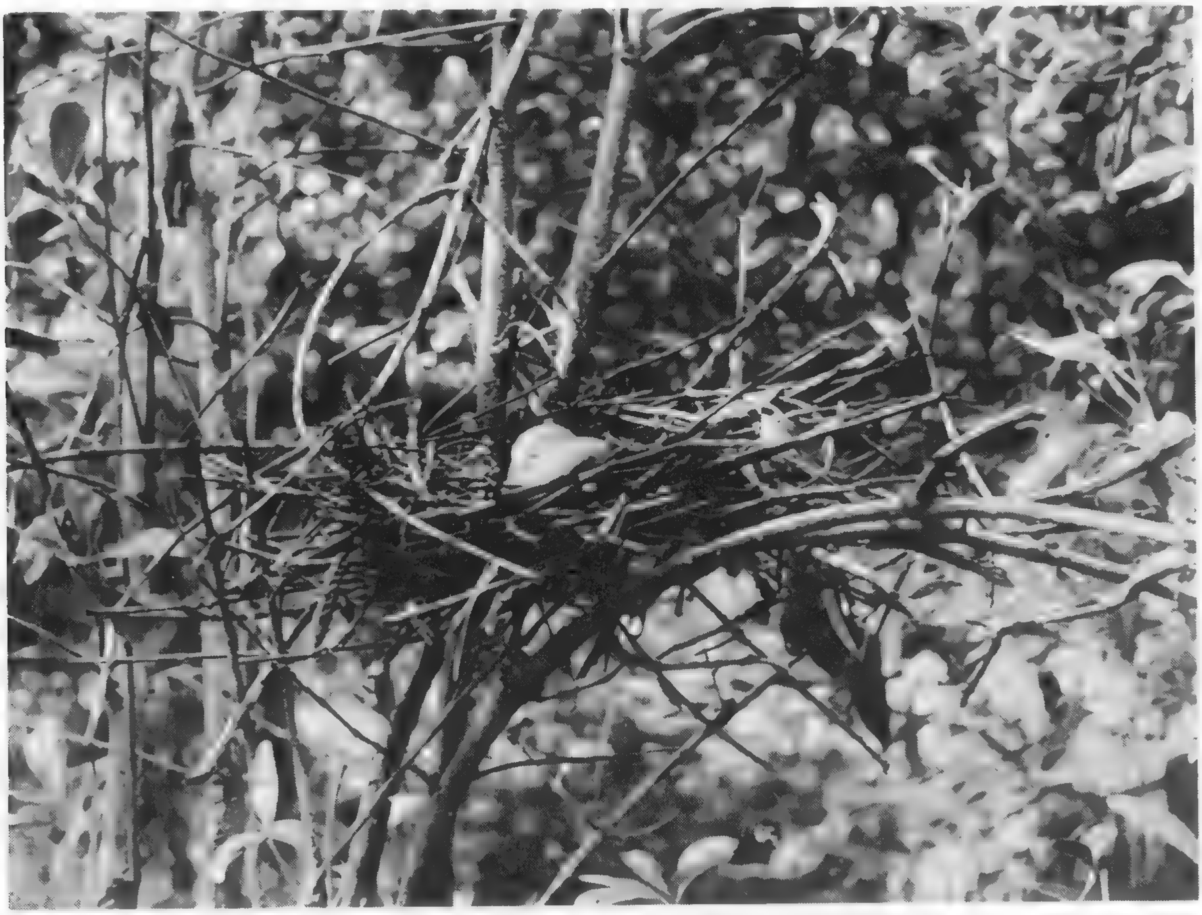


Figure 5 (*above*). A sturdy ibis nest constructed in the thick mangroves.

Figure 6 (*below*). A flimsy nest. Such nests often fail to withstand the heavy winds accompanying tropical storms. Photographs by F. Haverschmidt.



ibises frequently add twigs to them even after laying the eggs. Most nests last only one season, hardly ever through the year.

Penard and Penard (1908) remarked that the Scarlet Ibis does not build a nest; instead, it takes over old herons' nests and even ejects smaller herons such as the Snowy Egret. We found no evidence to support the latter statement, but since the Scarlet Ibis in Trinidad now tends to breed later than the herons, it probably uses heron nests in some instances. Conversely, the Cattle Egret, a newcomer, has occasionally taken over a Scarlet Ibis nest, possibly after the latter abandoned its eggs.

We do not believe it possible that the Cattle Egret will ever overcrowd the Scarlet Ibis, as some have feared. Most ibis colonies exist in large areas of mangrove where there is ample room for Cattle Egrets and all other herons besides. The different species associating together in the colony place their nests at most any elevation—in the case of herons from six to 35 feet above high water—the height depending on the type of branches available. Although all the species occupy the same area, each species tends to be separate, with several nests together in groups of 10 to 15 on one branch. A group with species intermixed is unusual. Scarlet Ibises and all the herons rarely build isolated nests, except for the less common Boat-billed Heron, which usually nests rather high in the trees. A nesting colony keeps together either as one unit or two or three closely connected units. Generally a nesting colony covers a wide area and holds a great many birds. One such colony encompassing five acres in Trinidad during 1963 contained over 2,500 nests of the Scarlet Ibis.

The Eggs

The ground color of the eggs varies from dull olive-green to buff, with dark brown markings. One hundred Scarlet Ibis eggs in the Penard oological collection from Surinam, preserved in the Leiden Museum, average 56.03 by 37.06 millimeters, with extremes of 65.3 by 35.5 mm and 50.2 by 42.9 mm, 48.05 by 34.06 mm and 55.9 by 33.4 mm (Hellebrekers, 1942). Twenty-one additional eggs, recently measured in Surinam, fall within these limits. The weight of thirteen fresh eggs averaged 44.8 grams, with the extremes 37.5 and 46.4 gm. Two dwarf eggs measured 31.2 by 27.2 mm and 35.6 by 27.6 mm, the latter weighing only 14.9 gm. Fourteen eggs collected in Trinidad average 55.3 by 37.6 mm, with extremes well within the limits of the Surinam eggs. Four Trinidad eggs averaged 40 gm in weight, ranging from 38 to 43 gm.

The clutch size in Surinam is almost invariably two eggs. On 27 August 1967, only four out of hundreds of nests contained three eggs. Of these four clutches, two had one addled egg. We never saw three nestlings in one nest.

By contrast, the Scarlet Ibis in Trinidad frequently lays two-egg clutches but more commonly three. Occasionally we found four eggs in a nest. Ibises lay eggs at intervals of one or two days, and incubate them for about 23 days. Both sexes share the incubation. The young hatch at intervals of one day or more. The incubation period for captive birds that bred twice in one season in an outdoor aviary in England (Risdon, 1969) was 21–22 days for two eggs.

Breeding Success

In Trinidad, nests with three in a clutch were not nearly as successful as those with two. One factor against three-clutch nests is likely competition for space. The nests often do not seem large enough or deep enough to accommodate three eggs, let alone three young. Figure 7 shows the hatching success of 15 nests, in which we knew the number of eggs and chicks. Less than half of the three-clutch nests were completely successful.

Nestlings from two-egg clutches show greater fledging success than do those from nests with three young. If only two of three eggs hatch, both young usually fledge. When all three hatch, the youngest nestling, considerably smaller than its siblings, suffers in competition for food and may be pushed out of the nest. At any age, falling from the nest is the most common cause of death. Figure 7 shows the fledging success of ten nests where the fate of the full complement of nestlings, except for one in a three-egg clutch, was known up to the time of fledging.

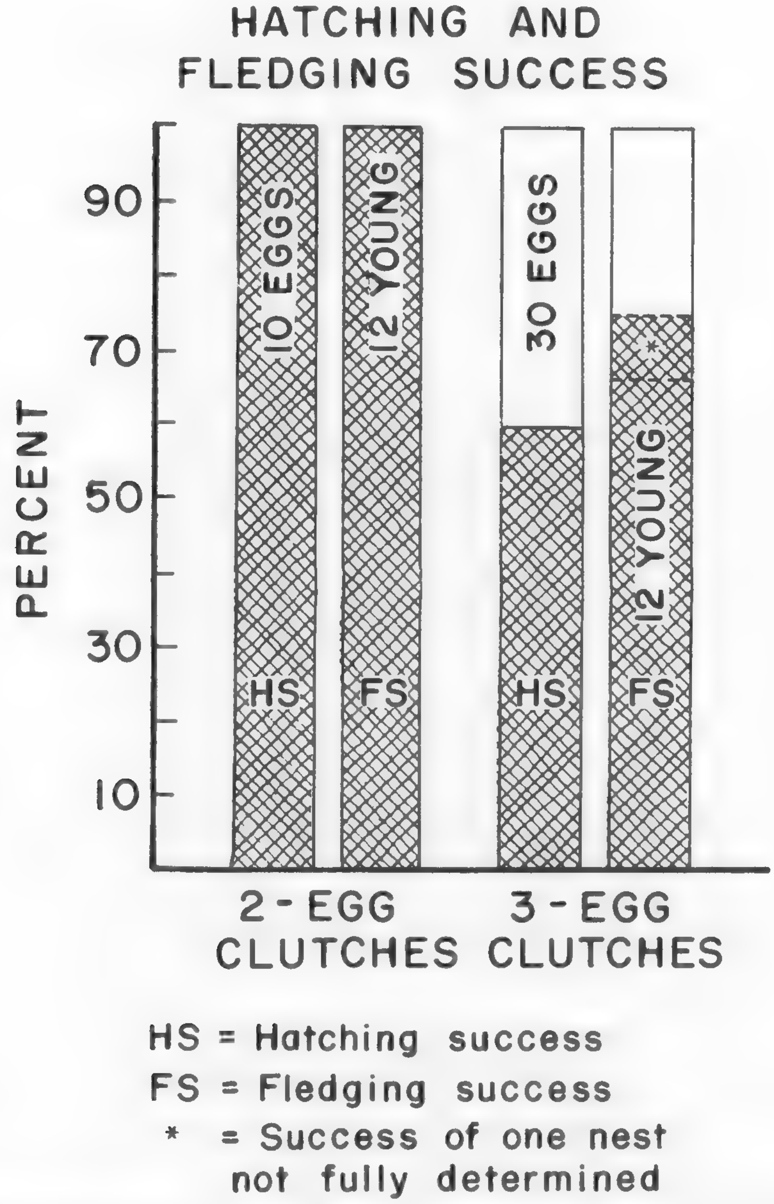


Figure 7. Three-egg clutches are rare in Surinam. In Trinidad they are much more frequent. Although the data presented above from Trinidad are meager, they indicate that two-egg clutches and broods of two survive much more frequently than nests with three eggs or young.

Development and Dispersal of the Young

It is difficult to obtain data on young Scarlet Ibises after they are 12 days old. If disturbed at about that age, they tend to move from the nest and fall from the branches. Thus, human disturbance in the mangroves at that time increases mortality rate of the young. Ibises of known age banded in Trinidad provide the details of growth in Table 1.

In general, very young nestlings are almost naked, with a little blackish gray down on the head and wings and sometimes a white tuft on the crown.

TABLE 1

Growth and Development of the Scarlet Ibis in Trinidad*

Age (days)	*Weight (gm)*	*Wing† (mm)*	*Longest primary‡ (mm)*	*Bill (mm)*	*Tarsus (mm)*
Hatching	27	20	—	18	16
1	47	24	—	22	17
2	57	28	—	22	22
4	80	32	6	24	26
8	178	45	13	30	28
11	195	72	25	36	40
16	over 300	120	55	49	56

†Wing measurement from carpal joint to wing tip.
‡Primary measured from tip to point of insertion of quill in socket.
*Weights and measurements represent means of seven birds.

CHANGES IN PLUMAGE AND SOFT PARTS DURING DEVELOPMENT

Age (days)	*Condition*
Hatching	Eyes shut, bill orange with black tip, egg tooth present, orbital area orange, legs flesh-pink, horny digital claws noticeable.
2	Eyes just opening, orbital area flesh-pink, legs flesh-pink tinged gray.
4	Eyes open, orbital area dull gray, legs dull pinkish gray, bill orange with black tip and other dark marks faintly showing.
8	Feather tracts visible.
11	Feathers sprouting on wings and body, head and neck downy, bill almost all dark with penultimate pink band.
16	Feathers all over, except head still downy. Primaries and tail sprouting, rump whitish. Bill darker but still with faint pink patches. Horny digital claws still present.
23	Feathers complete, both gray and white. Can flutter from branch to branch.
25	Could almost fly.

Their bill is pinkish orange and black and not decurved. Though fairly silent for the first week, they give a squeaky whistle thereafter. To feed, they thrust the bill into the adult's gullet as the latter regurgitates. The young defecate over the edge of the nest. Haverschmidt noted in Surinam that nestlings pant when exposed to direct sunlight and cannot endure it for long.

Although most young birds in Trinidad seem capable of flight at about four weeks of age, they do not always fly then. They may be five or six weeks old before leaving the trees. The captive birds in England left the nest at 40 days of age and first flew after about 52 days.

At twelve days of age well-nourished young can leave the nest; if undisturbed, they probably stay in it longer. After leaving, they move about in the mangroves, using their bills and wings as well as legs for climbing. If they fall in the water they can swim a little. When about three weeks old they tend to concentrate in flocks fairly high in the trees where the parents go to feed them. Separation from their parents may be a significant cause of mortality among these older young. In Trinidad, ffrench found many dead chicks, aged from two to three weeks, below nests in tall trees.

In Surinam, too, the young disperse from the low mangrove forests. They move in large numbers along small creeks or on the mud below the tall mangroves, not straying far from the trees.

By banding young at the nest, we have established some additional facts about their dispersal. Figure 1 shows the recovery localities of 16 of 1,500 young ibises banded at Gandoe, Surinam (500 in June–August 1966; 1,000 in July–October 1967). It is clear from these records that the young birds scatter rather widely. Table 2 shows that some, recovered within five months of banding, were more than 150 miles away from the home colony; others remained close by. The most distant record was that of an ibis recovered about 280 miles from its nest only seven and one-half months after banding.

In Trinidad, 131 young were banded at Caroni, 54 in June 1963 and 77 in September–October 1965. We have two recoveries: one still in the colony five months after banding; the other 200 miles west of Caroni, near the Gulf of Cariaco and Laguna Campona on the northeastern coast of Venezuela 13 months after banding.

Plumage and Molt

The adult is completely bright scarlet with the longest four primaries tipped blue-black. It is somewhat paler on the head, neck, and underparts. The bare face and legs are pinkish red; and the bill appears to vary from pinkish brown or horn to almost black, the blackish color possibly being correlated with the breeding season. The post-breeding molt occurs in Trinidad between October and November, three or more primaries being molted simultaneously. In Surinam an adult male collected in the colony was molting on 7 July 1966.

The immature plumage is generally a dull grayish brown on the head, neck, and upperparts, and white on the lower back and underparts (see Plate I). The bill is brownish orange. Molt into adult plumage is a lengthy process, being known, from banding recoveries in Surinam, to begin as early as the fifth month after hatching. At this stage a few pink, orange, or even red feathers appear. One specimen, banded when ready to fledge in October 1967,

TABLE 2

Recoveries of Scarlet Ibises Banded in Surinam

*Locality No.**	*Band No.*	*Date banded*	*Date recovered*	*Place of recovery (coordinates in parentheses)*
1	696-81633	7 July 1966	16 Mar. 1968	NE of Paramaribo, Surinam (5.5 N. 54.5 W)
2	696-81787	24 July 1966	25 Jan. 1968	Coronie, Surinam (5.5 N 56.1 W)
3	736-37099	1 Oct. 1967	3 Dec. 1967	NE of Paramaribo, Surinam (5.5 N 54.5 W)
4	736-37045	1 Oct. 1967	19 Nov. 1967	near Paramaribo, Surinam (5.4 N 55.0 W)
5	736-37290	10 Oct. 1967	15 Mar. 1968	near Paramaribo, Surinam
6	736-37353	10 Oct. 1967	7 Feb. 1968	Calcutta, Surinam (5.5 N 55.8 W)
7	736-37268	10 Oct. 1967	Sep. 1968	Kourou, Fr. Guiana (5.0 N 52.3 W)
8	736-37363	10 Oct. 1967	6 Feb. 1968	Iracoubo, Fr. Guiana (5.2 N 53.1 W)
9	736-37356	10 Oct. 1967	11 Feb. 1968	Iracoubo, Fr. Guiana
10	736-37310	10 Oct. 1967	1 Mar. 1968	Sinnamary, Fr. Guiana (5.2 N 53.1 W)
11	736-37236	10 Oct. 1967	10 Nov. 1967	Sinnamary, Fr. Guiana
12	736-37212	10 Oct. 1967	29 May 1968	Montagne d'Argent, Fr. Guiana (4.2 N 51.4 W)
13	696-81540	7 July 1966	Feb. 1969	Wageningen, Surinam (5.4 N 56.4 W)
14	736-37427	10 Oct. 1967	15 Mar. 1969	Sinnamary, Fr. Guiana
15	736-37031	1 Oct. 1967	9 July 1969	Pointe Isère, Fr. Guiana (5.4 N 53.5 W)
16	736-36959	1 Oct. 1967	10 Feb. 1969	Macouria, Fr. Guiana (4.5 N 52.2 W)

*See Figure 1 for locations of recoveries.

showed many pink feathers when collected in French Guiana on 1 March 1968 (see Table 2, number 10). The scarlet color appears very gradually, becoming fully acquired when the bird achieves definitive adult plumage at about one year of age. In rare instances (e.g., male taken at Coppenamepunt, Surinam, on 6 June 1948) adult birds wear an entirely pink plumage with no trace of scarlet and no remnants of the brown plumage of the immature. The evidence suggests that individual birds become fully scarlet at different rates. In view of the protracted breeding season and our lack of data from banded birds of known age, we cannot be more specific about the exact age of plumage change.

Examination of many specimens of immature birds in transitional plumage indicates that the order of molt is as follows: The mantle, scapulars, sides of breast, upper and under tail coverts, lesser wing coverts, and central rectrices begin molting first, followed by the white plumage of the lower back and breast, which becomes pinkish or orange, and finally, the rest of the plumage, with the feathers of the head and neck the last to change.

While definite information from birds of known age is lacking, we believe that the Scarlet Ibis first breeds in its third year of life (C. F. Bundy, *in litt.*). We have never found breeding birds with any trace of immature plumage.

In an experiment to investigate the possible conspecificity of the Scarlet Ibis and the White Ibis (*Eudocimus albus*), Bundy (1965) placed Scarlet Ibis eggs from Trinidad under nesting White Ibis in Florida. A few scarlet birds reached maturity and some of them subsequently mated with white birds. Although none of the offspring from these matings was banded, the appearance of several pink birds among them indicates the likelihood of successful hybridization (Zahl, 1967). Gray (1958) had earlier reported hybrids produced from among captive birds. The White Ibis does not normally occur in either Surinam or Trinidad, though an individual was seen in the Caroni Swamp in 1964 (ffrench and ffrench, 1966).

Measurements and Weights

Statistics of 20 birds in Trinidad (Table 3) show that males tend to be larger than females in all respects. The weights of birds taken in Surinam indicate greater variation according to climatic conditions. During droughts an adult male weighed as little as 415 gm, while a female weighed 483 gm. Maximum weights at other times were 890 gm for a male, 855 gm for a female. Five males averaged 683 gm and ten females 595 gm.

Two young birds just out of the nest weighed 455 and 545 gm, while a nearly fledged bird in the nest weighed 495 gm.

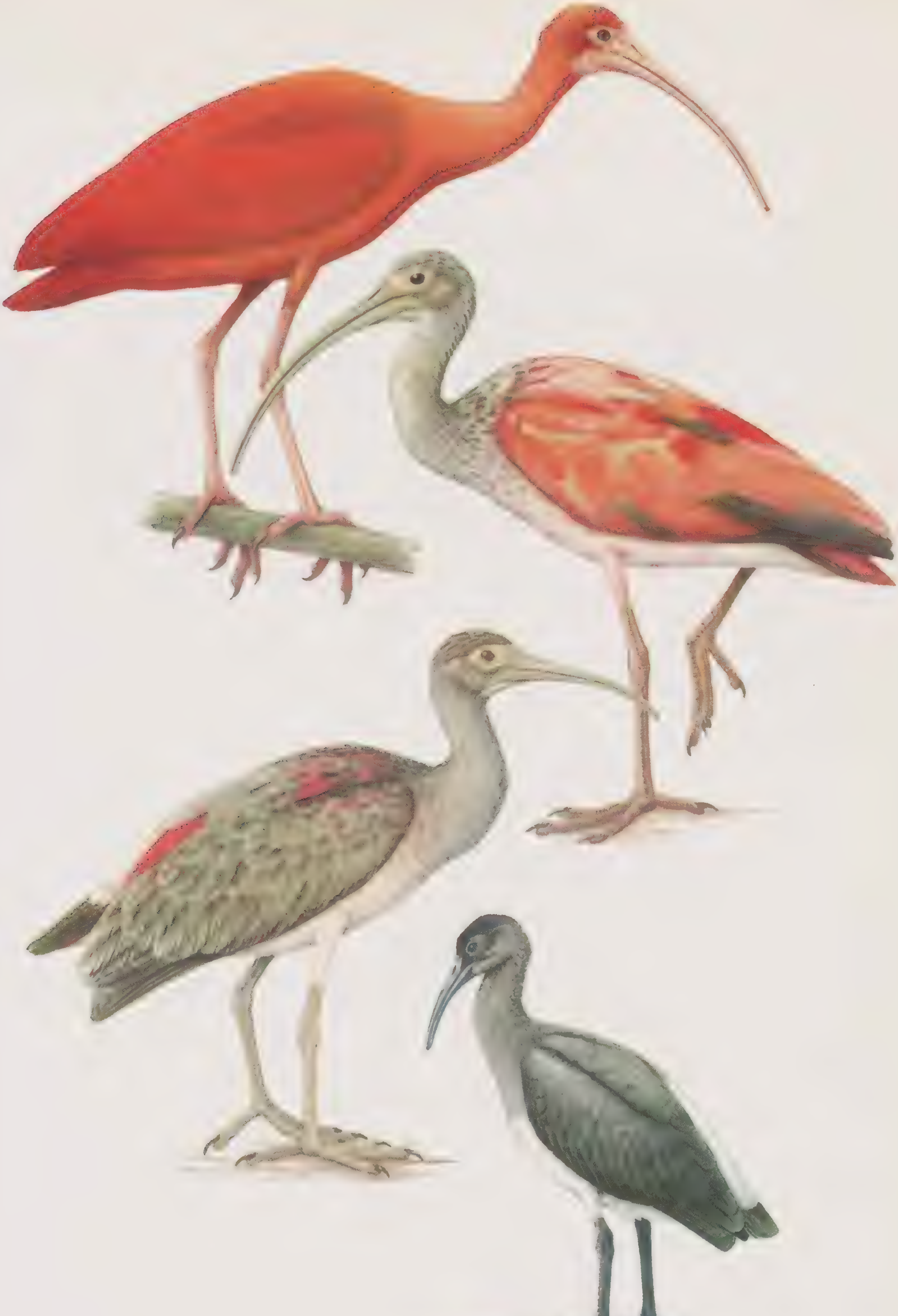
General Habits and Behavior

In a usual day's activity Scarlet Ibises leave the communal roost early in the morning, going in large flocks which soon break up to feed on the open mud flats when the tide is low, or in the thick mangrove forest when the tide is high (Figure 8). During the day the birds are often hard to find; but occasionally one sees a large flock as it moves from one feeding place to another.

About one hour before sunset flocks begin to approach the roost, flying in intermittently until after sunset. The numbers in each flock vary from a few to 60, the average being 15 to 20. Sometimes several flocks combine near the roost to form one large one. They either fly in a V-formation or in an irregular skein, alternately gliding and flapping their wings.

Ordinarily the birds use the same roosting site each night, but they sometimes extend it to include the surrounding mangroves. Occasionally, perhaps due to human disturbance, the birds roost in two or three major groups. Though separated by several hundred yards, the birds in one group constantly commute to another. At the roost, ibises do not tolerate human approach closer than 75 yards. Once they have settled in the roost, they move about very little and seldom call, but from close quarters one can hear them uttering soft, plaintive, rather high-pitched notes, quite distinct from the croaks and quacks of the herons with which they associate.

Plate I. The Scarlet Ibis (*Eudocimus ruber*) in various plumages, from a painting by Paul Barruel. *Upper left,* adult male in fresh plumage, Leonsberg, Surinam River, 3 February 1966. *Upper right,* female in intermediate plumage, Maasstroom, Commewijne District, 19 December 1965. *Lower left,* male in very worn intermediate plumage, Leonsberg, Surinam River, 27 February 1964. *Lower right,* nestling about to fledge, colony near Gandoe, Surinam, 5 August 1966, Birds illustrated here are from specimens in the Haverschmidt collection in the "State Natural History Museum" at Leiden, Holland.



Owing to the awkward location of the nesting colonies in tidal mangrove forests, we were unable to study adequately the behavior of adults at the nest.

Conservation

The governments in Surinam and Trinidad have provided some protection for the Scarlet Ibis, partly because of their potential value as a tourist attraction. This has not always been so.

Long before European settlers arrived, Indians probably hunted the Scarlet Ibis in northern South America. Kappler (1881) describes such a raid by the Indians of Galibi, west of the mouth of the Marowijne River, in what is now the Wia Wia Reserve in Surinam. Hunters commonly shot ibises at the roost and as they flew to their nests. Quite recently, in 1948, baskets full of nestling ibises were on sale in the Paramaribo market; and, in 1952, a corral of mangrove sticks, an assembly place for captured nestlings, was found in the mud at the Coppenamepunt colony.

TABLE 3

Weights and Measurements of Scarlet Ibises in Trinidad

Measurements	*Males (8 birds)*			*Females (12 birds)*		
	Range	*Average*	*Standard deviation*	*Range*	*Average*	*Standard deviation*
Weight (gm)	710-770	741	21.5	560-640	603	27.5
Wing (mm)	260-275	266	5.5	231-262	247	8
Bill (mm)	150-176	165	8	116-138	132	7
Tarsus	79- 91	85	4	67- 80	74	3.5

In 1953 the Coppenamepunt area was closed to all hunting; in 1954 a new game law protected the Scarlet Ibis throughout the year; and in 1966 the Coppenamepunt became a nature reserve. That year the nesting colony moved to the Gandoe area. Also in 1966 the government set aside the Wia Wia Nature Reserve, 140 square miles of coastal swamp in the region of the Marowijne River, and closed it to hunting. The relative inaccessibility of this reserve may well protect the Scarlet Ibis more effectively than any man-made regulations. The illegal shooting, of which unfortunately there is still a great deal in the country, is not generally in the vicinity of the nesting colonies.

In Trinidad, too, the Scarlet Ibis was regularly hunted during much of the 1800's and in this century as well, rarely breeding undisturbed until 1950 when the Trinidad government appointed four game wardens to patrol the 7,900 acres of the Caroni Swamp. In 1953, a sanctuary consisting of 337 acres in a swamp favored by the species was declared a "prohibited area" to all persons except those holding special passes. Here the Scarlet Ibis bred successfully in 1953 and subsequent years. When in 1966 the ibis established a breeding colony a mile or two farther south, the government set aside another prohibited area of 207 acres to accommodate them. The authorities are presently considering the possible extension of the sanctuary to link these two areas.

The season for hunting game birds in Trinidad opens on 1 November and on that day each year a large body of hunters go out to hunt in the Caroni Swamp. As many as 500 Scarlet Ibises were often shot on this first day of the season, with smaller numbers thereafter, all outside the sanctuary areas. Under the supervision of the game wardens a bag limit of five Scarlet Ibises per hunter was set for each day. In 1962, when Trinidad achieved political independence, the Scarlet Ibis became the national bird of Trinidad and on 29 September 1965 it was declared totally protected.

Public opinion in Trinidad now seems to favor protection and a thriving tourist industry has built up, allowing some thousands of visitors annually to watch the great flocks assemble at the roost, indeed a spectacular sight. Some poaching still takes place, especially in unpatrolled areas, such as the Oropouche Swamp.

In spite of these very salutary measures in Surinam and Trinidad, we can have no cause for complacency when we consider the facts that no colonies have been located in Guyana for ten years, that the Scarlet Ibis is shot on sight in French Guiana where no game laws exist, and that it is already on the list of birds threatened with extinction in Brazil (Sick, *in litt.*). In Venezuela, too, the species occurs mostly in remote parts of the country where the few inhabitants care very little about protective legislation.

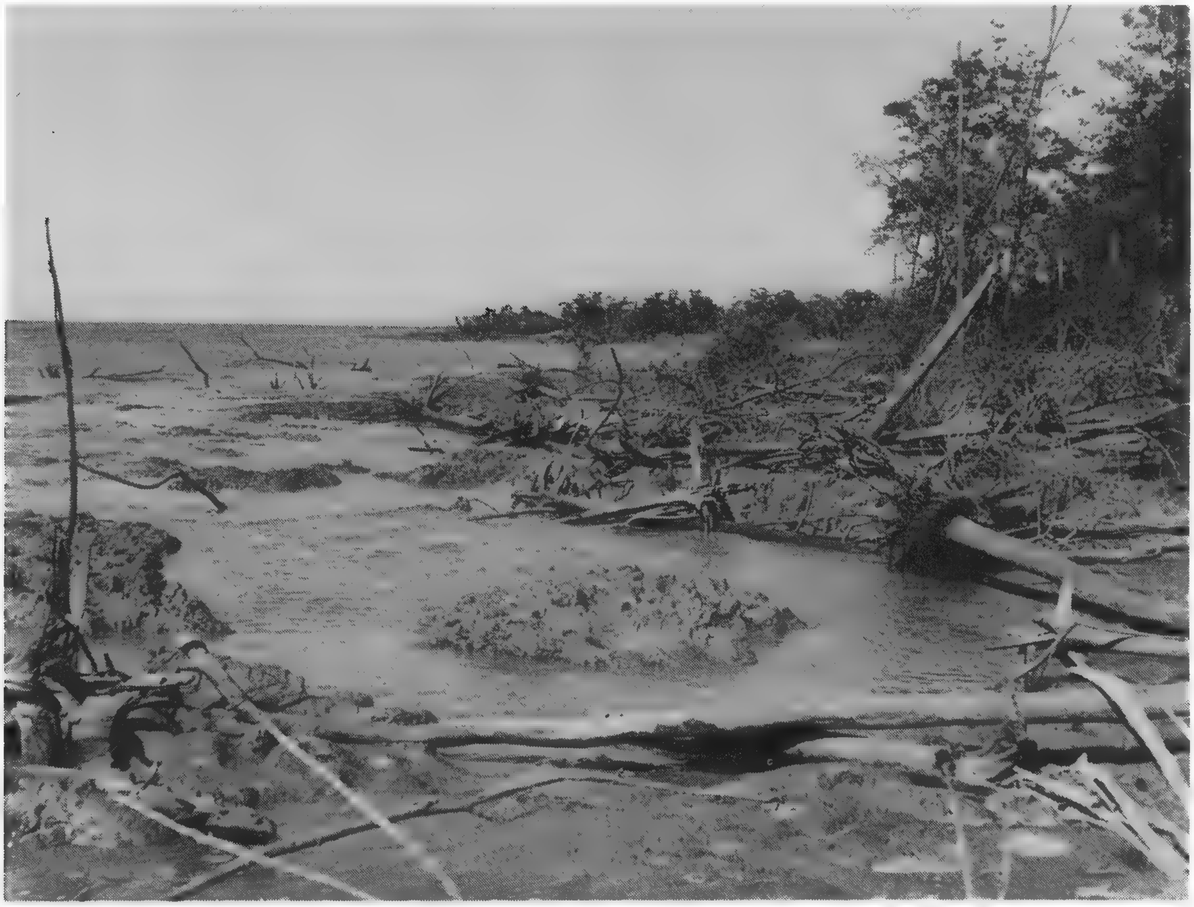


Figure 8. Coastal mudflats west of the mouth of the Surinam River, a favorite feeding place for the Scarlet Ibis. Photograph by F. Haverschmidt.

Summary

This paper contains results of studies of colonies of the Scarlet Ibis (*Eudocimus ruber*) in Surinam and Trinidad, with emphasis on the mangrove swamps at Gandoe in Surinam and at Caroni in Trinidad. Breeding appears to be spasmodic at some colonies; the Caroni Swamp colony has bred annually since 1953, except for 1964 and 1968.

Sixteen recoveries of 1,500 birds banded at Gandoe, Surinam, show that some immatures disperse for considerable distances along the coasts. The most distant recovery is from French Guiana, about 280 miles from the natal colony; one bird from Trinidad was recovered in Venezuela.

The Scarlet Ibis often roosts and nests in company with most of the herons common in the two countries. Predators include a water rat (*Nectomys*), and possibly the Greater Ani (*Crotophaga major*), the Long-winged Harrier (*Circus buffoni*), and the Yellow-headed Caracara (*Milvago chimachima*). The Scarlet Ibis was hunted regularly prior to the recent passage of protective legislation in both countries. The food of the ibis includes crabs, molluscs, insect larvae, and fish. During the breeding season adults move from saltwater areas to freshwater marshes for foraging.

The Scarlet Ibis breeds in the rainy season, but nesting often covers a lengthy period and is not definitely triggered by the onset of heavy rains.

The breeding site is often shifted to a new locality, usually within a few hundred yards of the old; but circumstances suggest that they may have moved one year to a site 40 miles away.

The nests, situated in mangroves, vary in height from a few feet up to 40 feet. They consist of dry mangrove twigs with fresh leaves added on top. They last one season. Though the Scarlet Ibis often nests in company with various heron species, each species tends to group its nests on separate branches. The colony keeps together, 2,500 nests being counted in one five-acre area in Trinidad.

The eggs are rather variable in appearance. Clutch size is usually two in Surinam, three in Trinidad, but the third egg rarely survives to hatch, and even more rarely does the third chick survive. The incubation period is about 23 days. Nestlings begin to climb about the trees at between two and three weeks of age. They can fly when about four weeks old, but probably do not do so until their sixth week.

Molt into the adult plumage may begin as early as the fifth month after hatching, and is complete when the young bird is about one year old. Captive birds, deprived of carotenoids, fade to a dull pink. Various experiments appear to indicate that the Scarlet Ibis is not conspecific with the White Ibis (*Eudocimus albus*).

During the day Scarlet Ibises disperse in flocks to feed on mud flats and in mangrove forests. In the evening they assemble at a communal roost.

The history of hunting and conservation measures in the two countries is outlined. In Surinam, indiscriminate hunting took place until a 1954 game law protected the Scarlet Ibis. In addition two of the colonies are now in nature reserves. In Trinidad, hunting prevented breeding until 1953, when the colony was protected as part of a sanctuary, prohibiting unauthorized

entry. In 1965 the Scarlet Ibis became fully protected, and is now Trinidad's national bird, being an important tourist attraction.

Acknowledgments

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The assistance of the Forest Department of the Trinidad and Tobago governments permitted the study of the ibis in the Caroni Sanctuary. The former Conservator of Forests, Mr. Hollis Murray, and the Game Warden, Mr. Roopchand Boodoo, helped and encouraged our project. Information and aid of various kinds also came from C. F. Bundy, Dr. P. R. Bacon, J. B. Saunders, R. A. Pallant, P. Schwartz, Dr. T. H. G. Aitken, and Dr. C. T. Collins. The Trinidad Field Naturalists' Club kindly financed the purchase of colored plastic bands. J. B. Saunders read a draft of this paper and offered several helpful suggestions.

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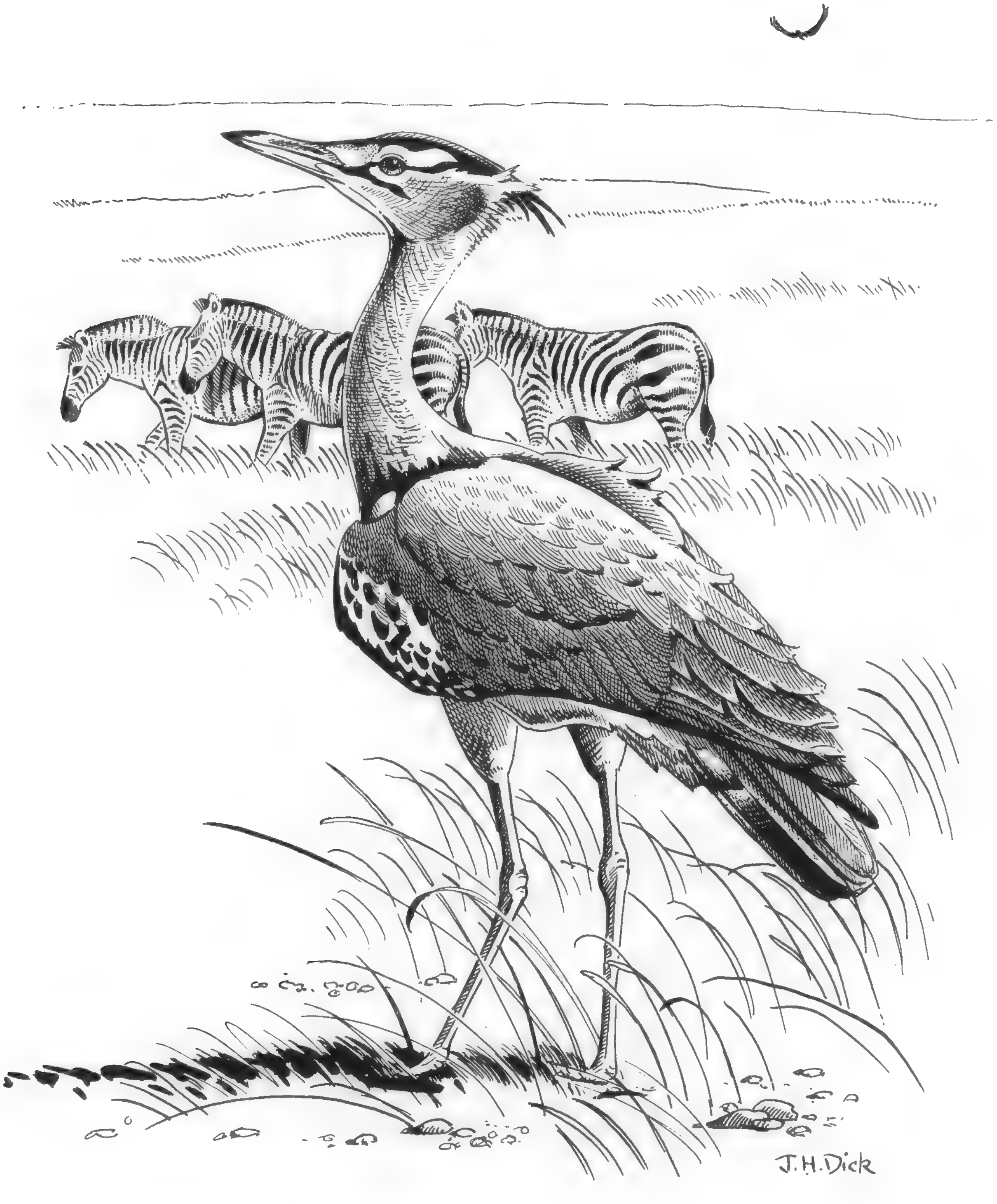


Kori Bustard, *Ardeotis kori*. Drawing by John Henry Dick.

BREEDING BEHAVIOR OF THE CATTLE EGRET IN COLOMBIA

DOUGLAS A. LANCASTER
Photographs by the author

The Cattle Egret (*Bubulcus ibis* = *Ardeola ibis*) is an eminently successful bird. It fills a niche distinct from other herons – feeding on insects and vertebrates found in fields where it associates with cattle. Its powers of dispersal are recalled repeatedly as an example of a species that in a matter of several generations spread, apparently without man's assistance, across the Atlantic to the New World. It has become one of the most common birds in some areas. In the Cauca Valley of Colombia, no bird of comparable size can match the Cattle Egret in numbers of individuals. And no species, large or small, is as conspicuous in the Valley where thousands of white birds fly out of several colonies shortly after dawn to feed in newly plowed fields or in numerous pastures with grazing cattle.

The literature records only a few breeding colonies in South America. Near the head of the Cauca Valley in Colombia, Cattle Egrets established two colonies over a decade ago. We suspect there is at least one other breeding colony there.

No other egret or heron has shown as much success at immigrating. Since its behavior and ecology had not been studied in detail, and since such investigations might provide answers to its spread and increase in numbers, I took advantage of an opportunity to study the Cattle Egret while in Colombia from September 1968 to August 1969.

I studied several aspects of the biology of Cattle Egrets in a colony situated on the Cauca River about five miles east of Cali, Colombia. From an observation post, about 20 feet above the ground in a tall bush at the edge of the colony, I could survey many of the birds with field glasses and telescope and watch their behavior. During the active period, I visited the colony three or four times weekly, usually between 08:30 and 18:00 hours. I selected several groups of nests for special observation, but made no attempt to mark individuals for recognition.

Color Changes of Soft Parts

The Cattle Egret shows no dimorphism between the sexes—both sexes look alike. The male may be slightly heavier, as is true in many other herons; but I have no data to support this supposition.

The breeding season is a long one, and during the colony's peak period of activity, one may see adult-sized birds whose unfeathered parts roughly reveal their age or breeding condition. In general full grown immatures have yellow irises and bill and black legs and feet. Breeding and non-breeding adults wear yellow legs, feet, bill, lores, and irises.

At the onset of breeding the irises, legs, and basal two-thirds of the bill turn red; the lores become a magenta to violet-magenta. The skin of the head and neck turns a cobalt blue. Both sexes show the same changes in the soft parts. These colors persist only for about two weeks, and then revert to yellow again. When the red color begins to change to yellow, it does so quickly, with the irises changing first and returning to yellow more rapidly than the other parts. The irises apparently never become wholly red; in birds viewed closely, a narrow yellow ring always existed as an outer circle of the visible portion of the irises. The bill, lores, and legs require somewhat longer to change. An intermediate stage of orange exists in the bill and legs of birds going out of the red phase. The bill assumes its yellow coloration while the lores and legs are still changing. Orange tarsi usually persist for several days after all the other parts have reverted to yellow. The color changes in the lores are more complex, showing more variability when changing from magenta to yellow than do the other parts. I recorded changes in the lores from magenta to pale pink to light gray or blue-gray to bluish yellow to yellow in a single bird. The irises may change from red to yellow while the bill, lores, and legs are still in peak breeding colors, or nearly so. On the other hand, I noted a number of birds undergoing simultaneous color changes in the bill, irises, and lores; but the irises always completed the change first.

A number of birds wore very intense breeding colors, undoubtedly an individual variation. The tarsi of these birds were such a dark red that they appeared black from a distance or in shadows. The irises were darker red and lacked the outer yellow ring. The bill, too, showed a very dark red hue with only pale yellow at the extreme tip.

The red coloration of the soft parts coincides with the initial stages of the breeding cycle. I have no data on the length of time involved for the soft parts to change from the non-breeding yellow to the reproductive red. All the birds I observed in the colony were already in peak breeding colors or were passing out of it as indicated by their activities.

Breeding birds probably show these color changes in the soft parts only for about two weeks, perhaps less, and individual birds vary considerably in the time required for the transformation. Usually, the change occurs rather rapidly. In one bird, just starting to build a nest, the colors included a red bill, magenta lores, red irises, and red tarsi. The intensity of the colors had begun to fall off, but the hues had not yet changed. By the following afternoon this bird had an orange bill, yellow irises, pale purplish lores, and red tarsi. Another pair exhibited peak breeding colors on 15 November. The next day

Figure 1. A view of the Cauca Valley looking toward the Central Cordillera north of Cali. The Cauca River flows in the foreground. These fertile fields with crops and cattle are favorite feeding grounds for the Cattle Egret.

the irises were half-red and half-yellow, and the magenta lores were paler. On 18 November, these birds wore completely yellow irises, yellow bills with the medial section orange, orange tarsi, and pale bluish yellow lores. I did not record the colors of these birds again until 21 November, when the pair showed all yellow soft parts. Still another bird in peak breeding colors changed in two days from red to yellow irises, magenta to purplish lores, and scarlet to pale red bill that was yellow-orange basally; but the legs remained red. Two days later this bird showed a golden yellow bill, yellow irises, pale bluish lores, and orange tarsi.

From these and many other observations, the minimum time involved for changes from the pre-incubation colors to yellow soft parts is as follows: irises, two days; bill, three days; lores, five to six days; tarsus, six days.

While the soft-part colors coincide with certain stages of the cycle, I observed considerable latitude. The change from reds to yellow generally occurs after pairing and during the construction of the nest. I have seen birds with yellow soft parts, except for red legs, just beginning to build a nest. A bird with orange legs and pale bluish yellow lores incubated, as did another with red-orange tarsi and pink lores. A number of birds assumed all yellow soft parts during the nest-building stage and several days before laying the first egg. One bird with almost peak breeding colors fed a two-week-old young that had a yellow-billed parent. This condition, in which mates manifest different colors, was noted frequently. It may represent different rates of change, but also indicates varying color conditions at the time of mating. If a bird with young loses a mate, the yellow-billed parent may form a new

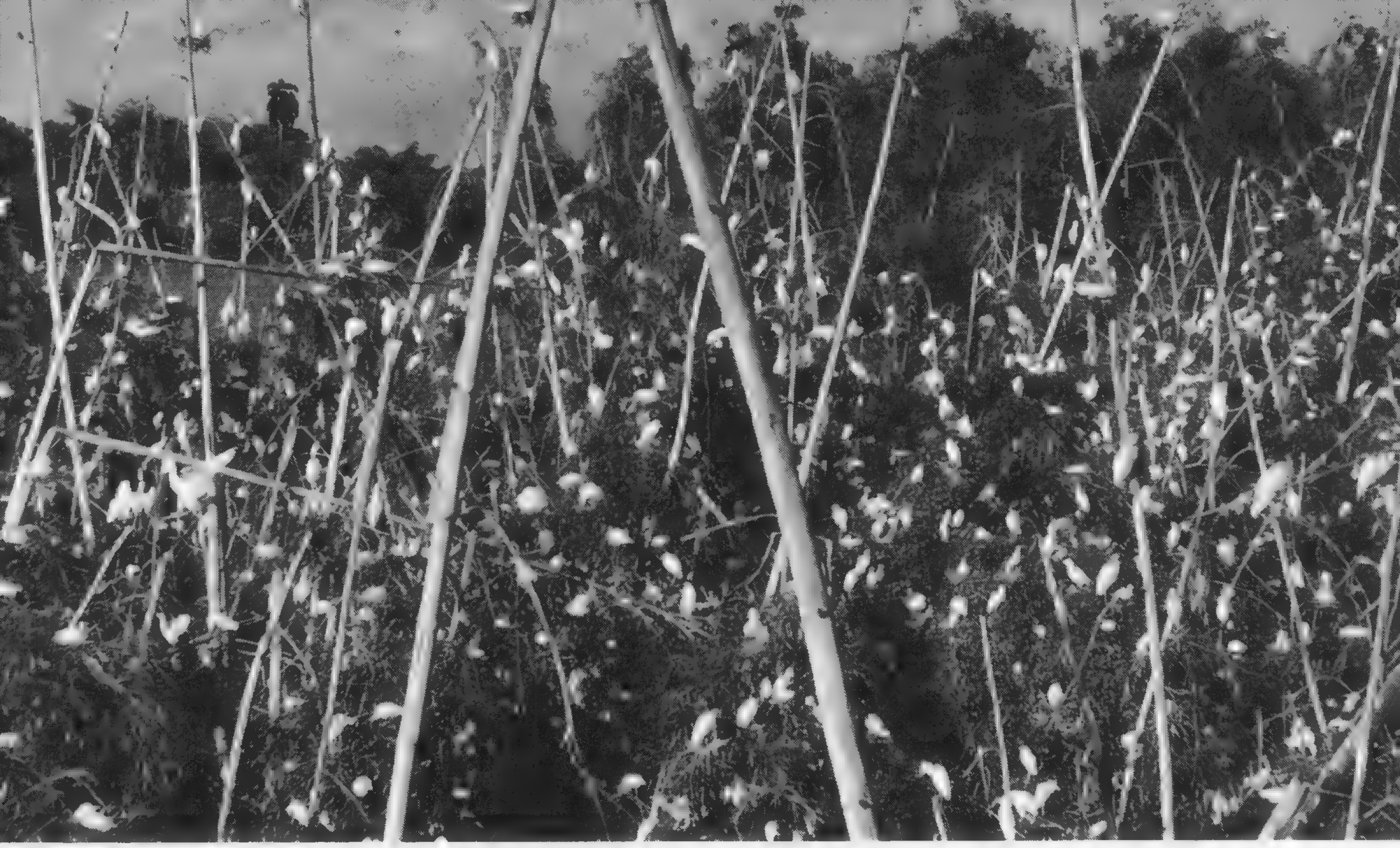


Figure 2. The colony of Cattle Egrets east of Cali along the Cauca River in which the study was undertaken. The photograph takes in only about 35 to 40 per cent of the colony. The egrets nest mostly in the bamboo, the dominant vegetation, which shows obvious deterioration from the many years of supporting thousands of egret nests. An untouched stand of bamboo, 30 to 40 feet high, can be seen in the right background.

pair-bond with a red-billed bird seeking a mate. I recorded several other pairs with different colors: a bird with peak breeding colors building a nest with its mate, a bird with all yellow soft parts except for red-orange tarsi; several courting pairs in which one bird wore peak breeding colors, and the other had all yellow soft parts; a bird with yellow soft parts standing in a completed nest with its mate in breeding colors.

Most, if not all, herons manifest a change during the breeding season in the color of the bill, irises, legs, lores, and eye-rings, or at least one or more of these parts (Abdulali and Alexander, 1952; Dement'ev, *et al.*, 1968; Gush, 1952; Meiklejohn, 1952; Meyerriecks, 1960; Palmer, 1962; Tucker, 1949).

Trends are apparent. Thus, birds with black soft parts generally exhibit no alterations in these parts except that the black may change from a rather dull tone to a more intense and glossy one. Yellow soft parts tend to change, if at all, to a yellow-orange, orange, or red. Changes in colors of the soft parts occurring in some North American Ardeidae are illustrated in the "Handbook of North American Birds" (Palmer, 1962) and discussed by Meyerriecks (1960).

In addition to these short-term changes that probably last for only two to four weeks, several herons reportedly manifest a "blushing" of the loral region and also the legs and irises during intense agonistic or sexual displays, during which the colors may change markedly (from yellow to scarlet in the Snowy Egret, *Leucophoyx thula;* neutral to scarlet in the Least Bittern, *Ixobrychus exilis*) and revert to their normal hues in a matter of seconds or a few minutes. Meyerriecks (1960) first described this "blushing" for the Snowy Egret and Green Heron (*Butorides virescens*) and Mountfort (1958) for the Cattle Egret in southern Spain. I did not record this phenomenon in the Colombian birds.

The soft parts change color in both male and female. And since the plumages are similar in both sexes, except in the bitterns of the genus *Ixobrychus,* the changes in colors worn during the early stages of breeding do not serve to differentiate the sexes. Meyerriecks (1960) points out, however, that in the four species he studied ". . . the males had much more brilliantly colored soft-parts and more lustrous plumage than did the females." This is not true for the Cattle Egrets in Colombia, where I could not detect any differentiating characters between the sexes except in behavior.

One assumes that since the soft parts change conspicuously for a short period at the beginning of the breeding cycle, the change to red must enhance pair-formation and provide a visual stimulus that—along with precopulatory displays—has greater effectiveness than yellow soft parts. This would be difficult to test experimentally, because, although one could change the color of the legs, lores, and bill with paints and dyes, the irises could not be altered from yellow to scarlet red.

Observational data, on the other hand, might indicate whether or not the red colors serve as greater visual stimulants during pair-formation provided that many birds, wearing yellow soft parts, also paired. A quantification of pairing success in birds with red and yellow soft parts could then be compared. Even these data would have to be treated cautiously, however; for if a reduced pairing success were apparent in birds with yellow soft parts, the lower success might also be attributed to a reduction in the intensity and number of displays. Both the changes of colors and behavior are, after all, caused by alterations in the blood levels of gonadal and pituitary hormones. As noted below, both intensity of displays and intensity of breeding colors correlate well with one another.

I did not collect sufficient data to make a correlation relating to pairing success and soft-part coloration. But I did notice several yellow-billed males displaying to attract mates—and succeeding. I noticed yellow-billed females occasionally mating with red-billed males. Several times I recorded a red-billed bird attending a nest with young and a yellow-billed parent.

Some experimental evidence is available to indicate that the increase in gonadal hormones causes the transformation of soft-part coloration in herons. Noble and Wurm (1940) demonstrated this relationship for the Black-crowned Night Heron (*Nycticorax nycticorax*). The male sex hormones, or androgens, produce their physiological effects by increasing the deposition of pigment and/or by increasing the blood flow through the production of an expanded capillary network in the peripheral, non-feathered areas.

Two specific incidents of pairing are noteworthy with regard to displays performed by some birds with yellow soft parts, and others with red soft parts. On 16 June, four males within an hour in midafternoon took up positions on the same bush within a few yards of one another. All four of these unmated males proceeded to display. Two males (Males A and B) had red bills, tarsi, and lores; Male A had yellow irises, Male B red ones. Males C and D had yellow bills and yellow irises. As many as ten females soon landed on bamboo branches in the immediate neighborhood of these males. One male (A) occupied a partially built nest; the others occupied branches without nests.

The two red-billed males manifested precopulatory displays with far greater intensity and frequency than the two yellow-billed birds. During several hours of observation not a single female flew to Males C and D. Male D eventually left the area. Male C attacked Male A twice in the same period. Clearly, the females showed a preference for high intensity displays by red-billed males.

Even the two red-billed birds showed differences in displaying. The females moved in on Male A (yellow irises) with greater frequency at first, for they subdued him much more quickly. Although Males A and B displayed with equal intensity, Male A showed considerably less aggression against incoming females. Male B (red irises) drove off all females during the period of observation.

I recorded only once a red-billed female moving in on a male with yellow soft parts (but orange tarsi). It did so although a male with red soft parts displayed only several feet away. In this case, the fact that the yellow-billed male had appropriated an intact nest, while the red-billed male displayed on a nearby branch without a nest, may suggest that the site—and especially the presence or absence of a nest—presents still another parameter influencing the choice of mate by a female.

Plumes and Their Variation

Cattle Egrets have buffy to salmon-colored plumes on the crown, breast, and upper back. These crest, pectoral, and scapular plumes function importantly in a wide variety of sexual and agonistic displays. The sexes show no difference in this character, but the length and the intensity of the color of the plumes varies greatly among breeding individuals in the colony. To determine the degree of variation, I recorded the condition of the plumes with respect to their length (none, medium, or long) and intensity of the salmon color (none, pale, medium, or intense). The crown was always buff or salmon-colored. Thirteen of 52 birds wore no crest plumes, 14 of 54 birds lacked scapular plumes, and 12 of 35 birds had no breast plumes. At the other extreme I recorded long crown, back, and breast plumes in 18 of 52, 19 of 54, and 8 of 35 birds, respectively. Sometimes I noted the female of a pair with long and intensely colored plumes and the male with obviously shorter plumes of medium or light intensity. At other times this condition was reversed. The long plumes and intense coloration do not necessarily go together although the data clearly show a tendency in this direction. Even so, some birds had long back or breast plumes of only a pale salmon color or no color at all. A bird generally showed roughly the same category, or intensity, of color and length of plumes in all three body regions. There were exceptions. One bird, Number 105, for example, wore long crown and back plumes but no breast plumes. Another, Number 115, showed crown plumes of medium length, very long back plumes, and no breast plumes. In still another, Number 108, the crown, back, and breast plumes were absent, long, and of medium length, respectively.

Breeding Behavior

During the breeding season the soft parts and plumage manifest no sexual dimorphism, indicating that sexual recognition is accomplished through behavioral displays. Although I had ample opportunity to watch birds feeding in fields, I observed courtship behavior only in the colony.

Birds in breeding condition may enter the colony at any time of the day, perch on an unoccupied branch in the tall *Ceiba* tree, on a stalk of bamboo, or on the tall bushes and proceed to display. Sometimes, males seeking mates remained in the colony in the morning; but most often they left with the vanguard to feed some miles away. All the birds returned to the colony in the late afternoon and courtship activity, on the part of unmated birds, reached a peak between 16:00 and 18:30 hours.

Agonistic Behavior

The behavior of an egret displaying red soft parts and ready to breed easily differentiates an unmated male from females. A courting male performs a number of displays that make him conspicuous. After arriving in the colony and perching, a male exhibits high-intensity aggressiveness toward all others. One can determine the state of hostility largely by the degree to which the bird erects its crown feathers: a fully erect crown indicates high-intensity

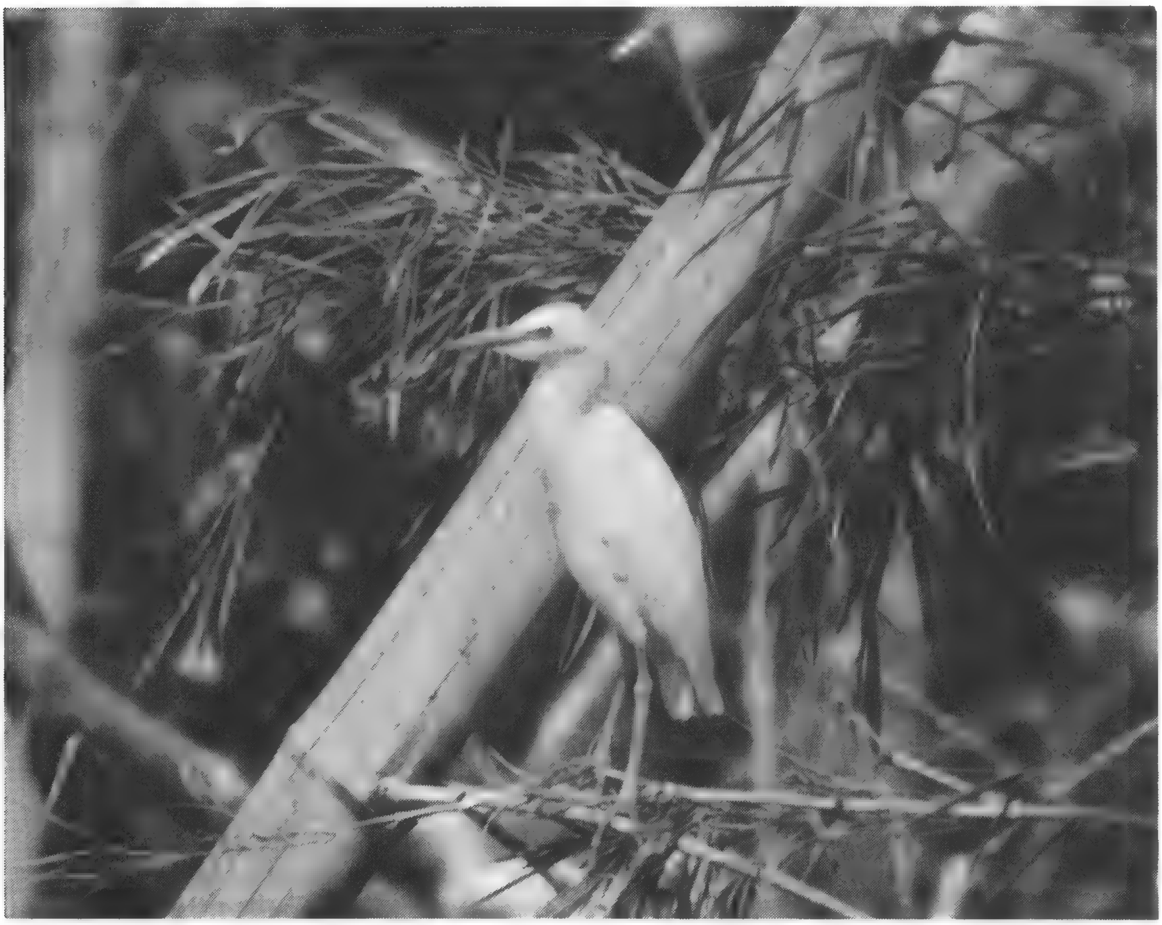


Figure 3. A breeding adult standing on a bamboo branch. This bird has scarlet irises, red legs and feet, and magenta lores. The basal two-thirds of the bill is scarlet red, the distal one-third yellow. Cattle Egrets in breeding condition wear these colors for only several weeks, reverting to bright yellow soft parts after pairing.

aggression and an appressed crown or crest indicates high-intensity fear. All degrees exist between the extremes. In the immediate area of a few square yards the male tolerates no other Cattle Egrets. The aggressive behavior involves a Forward in which the male stands erect with neck extended vertically and bill pointed at the antagonist. The feathers of the neck, face, gular region, crown, and breast are erected and the scapular plumes spread laterally and raised slightly. A highly aggressive male, in addition, usually holds the wings partially open and away from the body, and gapes the bill. A Cattle Egret, when manifesting lesser degrees of hostility, may hold the wings closer to the body, retract the head and neck somewhat, keep the bill closed instead of gaped, hold the scapular plumes against the back, and maintain a partially —not fully—erected crest and neck plumage.

The Upright is a typical hostile display of relatively lower intensity than the Forward, in which, as the name implies, the egret assumes an erect position with extended neck, faces the object of hostility, raises the crest, keeps the bill closed, and the wings against the body.

As in many other species of birds, the fluffing out of the body contour feathers, in conjunction with an outstretched neck and erect body, serves to make the displaying bird look as large as possible.

The aggressive Forward and Upright appear in full-grown immatures and breeding and non-breeding birds of both sexes; but an unmated male in breeding condition shows more aggression than at any other period of the annual cycle. At the time of pair-formation, and during the period immediately following, the female becomes equally aggressive, if not more so, in defending the nest site. During incubation the Forward becomes ritualized between adults of adjacent nests, often taking place from a sitting or crouched position and consisting of a series of sudden and alternating stabs by the contesting pair. I never saw either bird being struck by its neighbor; one antagonist always withdrew its head as the other one lunged out with its bill. This see-saw ritual occurred most often as one bird returned to its nest while the adjacent nest-holder sat on eggs or brooded young. The sudden activity stirred up by the incoming bird caused its neighbor to display aggressively in an encounter that only lasted for a matter of seconds and seldom involved more than five to ten sudden, alternating stabs by each bird.

In addition to the Forward, another display, the Head-flick, is common in agonistic encounters. A series of sudden, small, horizontal head movements occurs in situations that suggest a conflict of tendencies. I saw it frequently in birds attacking and defending a nest, in both adults and immatures, in ritualized Forwards between adjacent nest-owners, and in general, in agonistic encounters among birds that were fighting.

Egrets supplanted one another frequently either by flying to an occupied, but non-territorial, perch or by walking along a horizontal bamboo branch toward another egret. Sometimes, the attacking bird approached with a Forward. At other times an egret advanced in a semi-crouched position with a raised crest (Supplanting-run of Blaker, 1969), but always directed the bill at its opponent.

In response to a Forward, Cattle Egrets assume a Withdrawn Crouch — a hunched position with legs flexed, head and neck withdrawn, and plumage appressed. A bird so displaying usually turns and walks or flies away from the male giving the Forward.

Threat behavior often carried the day, but fighting occurred rather frequently in situations involving pair-formation and the appropriation of occupied nests. Then the egrets struck blows at the head and maintained balance and flailed at each other with beating wings. They always jabbed with necks extended upright and attempted to strike from above. Sometimes one bird flew up to meet an attacker, the two fluttering and fighting all the way to the ground. Such attacks were often vicious, leading to bloodied heads, faces, and bills.

Courtship Displays

Agonistic behavior is more highly developed during the breeding season than at any other time of the annual cycle. This generalization, of course, applies to all birds. It is not surprising, therefore, that displays typical of pair-formation and pair-bond maintenance often contain components of agonistic behavior.

The aggressive feather posturing, often with wings hanging slightly down and open, along with the red soft parts, reveals the displaying bird as an unmated male. The erected feathers on the neck reveal a conspicuous line of cobalt-blue skin along the back of the neck. The unpaired female, by contrast, maintains a compressed plumage. Once he selects a site, the male maintains an aggressive stance (Forward) even though no other birds are in his immediate vicinity. During this pre-pairing period the male establishes a considerably greater individual distance than at any other time, a distance that shrinks after pairing and gradually decreases further as nest-building and incubation proceed. The harsh *raa* call, typical of the Forward, changes to a more muffled *thonk* during the pre-pairing period (Blaker, 1969).

In his newly selected site, the courting male now performs several displays—visual signals—that include the Stretch, the Twig-shake, the Wing-touch, the Forward-snap, the Flap-flight, and the Forward. I have mostly used the terminology of Meyerriecks (1960) and Blaker (1969) for displays. These displays often begin when there are only yellow-billed, incubating birds in the vicinity and thus are not necessarily released by the presence of females. Within several minutes, however, one or more red-billed, unmated females fly to a nearby perch to observe a displaying male.

Stretch.—The male extends the neck vertically, or nearly so, and holds the head and bill at approximately 50 to 75 degrees off the horizontal, the body 40 to 50 degrees. He partially withdraws the head and neck onto the shoulders and simultaneously flexes the legs and lowers the breast nearer the perch. He then resumes a standing position and lowers the bill horizontally. At the bottom of the bow, the plumes of the back are erected and spread laterally. During the head and neck withdrawal, the bill remains directed upward. Males often hold the bill slightly open and often erect the feathers of the crest, neck, face, and gular region. The entire performance is a smoothly performed display. Blaker (1969) describes the accompanying call as a soft, crooning *rooo*. The male continues the Stretch after pairing, usually as part of the greeting ceremony. The female engages in a Stretch, but only after pairing, and then

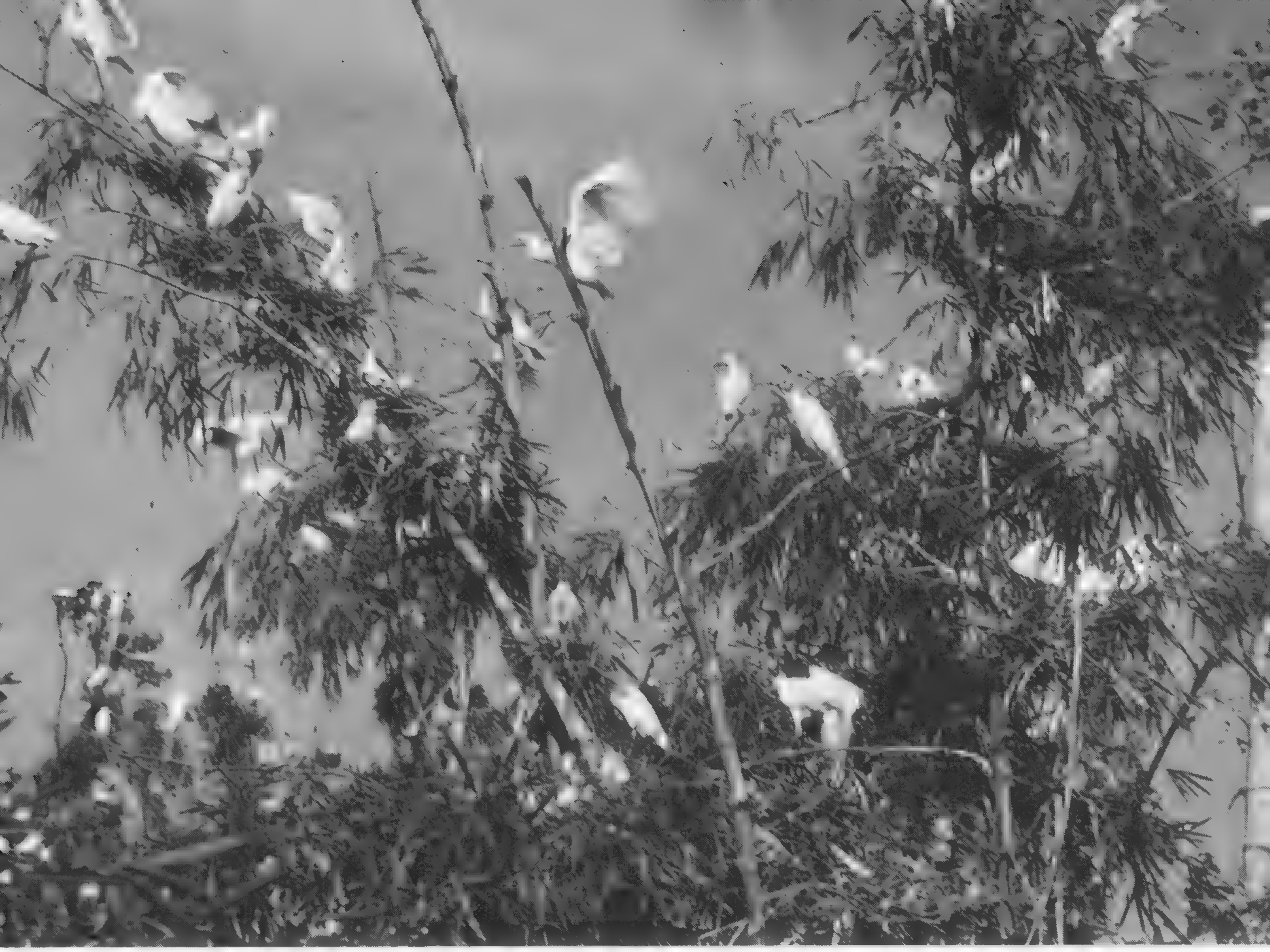


Figure 4. A closer view of a few stalks of bamboo showing the density and proximity of nests. Most of the birds in this photograph are nesting adults.

usually as part of the greeting ceremony at the nest and frequently prior to copulation. As incubation proceeds, the frequency of the Stretch in both sexes declines. Paired males and females generally perform the Stretch with less intensity than unmated males. Furthermore, I did not record this display with feathers of the crown and neck erected in the female. The paired male frequently keeps these feathers compressed, or only slightly erected. The Stretch seems to function to attract females prior to pair-formation, to invite the male to copulate after pairing, and to strengthen the pair-bond as part of the greeting ceremony. This display, conspicuous as it is, plays a more important role following pair-formation than preceding it. Single males perform it infrequently. The Stretch contains less of an aggressive component than some other displays. The Stretch probably originated from flight intention movements, to which it shows some obvious similarities. Meyerriecks (1960) and Blaker (1969) discuss this display, and those that follow, more fully.

Twig-shake.—Unmated, displaying males Twig-shake frequently. They extend the neck toward a twig or leaf above or below their perch, grab it with the bill, and shake it with a short series of quick, horizontal head movements that last from one to two seconds. Twig-shaking appears to be nest-building behavior given out of its regular context, for the movements are similar to those shown by both male and female when working on a nest. Erected feathers of the crest and neck are characteristic of this display. Sometimes only one twig is available. If a choice can be made, the male grabs a twig slightly above his head more frequently than one below, or near, the level of his perch.

I also noted the Twig-shake in an agonistic situation other than the one involving an unpaired, courting male: just after a bird at the nest had driven off an attacking adult or when two neighboring birds on nests had just completed a bout of sparring. In this context, the display seems to represent redirected aggression and clearly is somewhat more exaggerated than the normal nest-building movements. I never confirmed whether both sexes Twig-shake. The females, if they perform this display at all, do so occasionally at the nest after sparring with a neighboring bird. However, many bouts of hostility occurred between birds of adjacent nests that involved no follow-up Twig-shake.

Wing-touch.—This display appears to have originated from preening behavior; in fact, it is a preening movement involving a single, rapid sweeping motion of the slightly open bill along much of the leading edge of one wing. Frequently the display involves two such movements in rapid succession. Blaker (1969) also noted this behavior in Cattle Egrets in South Africa. No author, apparently, has recorded the Wing-touch in any other heron. It could easily be overlooked as a preening movement. And while it resembles displacement activity in that it appears to be a preening movement out of context, it appears to be an exaggerated and ritualized behavior, unlike a displacement activity. I observed it only in males prior to pairing.

Forward-snap.—Males displaying on perches, prior to mating, undergo a ritualized aggressive behavior directed at birds that are often a considerable distance away and that offer no obvious threat to the displaying male. The recipients of this display may be interested females on a perch five or more feet away; birds on a perch well out of reach that have paused in their flight through the colony; and even incubating birds dozing in their nest some ten feet away. The display, with neck and crest feathers erect, involves a single stab, extending the neck and withdrawing it. The neck often is not fully extended and the displaying bird stabs mostly downward. More significantly, however, the Forward-snap is slower and more deliberate than the rapid staccato action of real fighting. Furthermore, when a bird flies or lands close to the displaying male, the action changes to the Forward, typical of these agonistic encounters, and may include one or more rapid strikes with the bill at the intruding bird. I saw only unmated males in breeding condition exhibit the Forward-snap, and did not record it in females. I maintained the word "snap" in this display because of its obvious homology with the Snap described by Meyerriecks (1960), even though the egret does not gape and snap the mandibles together.

Flap-flight.—Unmated males exhibit this aerial display most commonly prior to pairing. It continues, however, for several days after the establishment of a pair-bond. Females show this display mostly, if not entirely, prior to pairing as they approach unmated males. In this display, the egret leaves its perch and flies to another one, roughly 10 to 50 feet away, or makes a circle and lands on the take-off perch. The wing-beats are slower and deeper than in normal flight, producing very audible "thump" sounds. The legs dangle diagonally behind and below the body. The neck is extended and held above the horizontal of the body, and the feathers of the neck and crown are erect.

TABLE 1

Number of Displays Performed by an Unpaired Male Cattle Egret*

Name of display or activity	*Total number*	*Average number of displays per minute*
Twig-shake	302	1.37
Forward-snap	140	0.64
Wing-touch	299	1.36
Flap-flight	61†	0.28
Stretch	9	0.04
Body-shakes	12	0.05
Preening bouts	12	0.05
Totals	835	3.80

*Total observation time—3 hours, 40 minutes. The figures do not include Forward Displays. The male maintained a Forward posture almost continually when not performing one of the other displays. During this period females made 12 attempts to land on the male. Four succeeded in landing but were dislodged and forced to leave immediately.

†Four of these flights were Circle Flights. Half (31) of the straight Flap-flights involved supplantings.

Forward.—With back plumes erect and spread laterally, and breast, neck, and crest feathers raised, males prior to pairing frequently turn around and walk up and down their perches with slow deliberate steps, their wings partly spread, bill slightly gaped, and neck partly extended or sometimes withdrawn. Blaker (1969) refers to this as the Wing-spread, but I cannot distinguish it from the agonistic Forward discussed earlier. The male maintains the Forward when not engaged in other displays on his territorial perch. In fact, the Forward (Wing-spread of Blaker, 1969) characterized the unmated male more than any other display. Both sexes give the display shortly after pairing when they arrive at the nest or nest site; but the male does it more frequently than the female.

Frequency of Courtship Displays

The six displays described above all comprise the repertoire of an unmated male in breeding condition. Most of the displays lack vocal accompaniment and clearly indicate the importance of visual cues in a colony of thousands of birds. The frequency and sequence with which the males give these displays varies. Table 1 shows the results of tabulating these displays in a male during three hours and 40 minutes of continuous observation one afternoon. The period was one of almost constant display. The male's crest, neck, and gular feathers stood erect almost constantly regardless of the activity, but I did not record these Forwards. The scapular plumes were spread most of the time. The only maintenance or comfort activities included 12 Body-shakes and a total of about five minutes of preening divided into short bouts. The red-irised and red-billed male performed the Twig-shake 302 times, more than any other display, but only several times more than the Wing-touch — 299 times. He exhibited the Stretch much less frequently — nine times — than the other displays although it is undoubtedly the most ritualized and conspicuous of the stationary behaviors. Several females observed the displays but made relatively few forays toward the male, which drove off females only 12 times during the 220-minute period. Of the 61 Flap-flights, four were circle flights, the male taking off and landing at the same perch; the remainder were straight flights, mostly to the same branch some 40 feet away. He supplanted other birds on 31 of the Flap-flights.

The male performed the various displays in no particular sequence. Figures 5, 6 and 7 show graphically the sequence and frequency of the various displays given by the same male during four 10-minute periods of the afternoon. The total number of displays varied from 40 to 70 for the four periods, Twig-shake and Wing-touch being by far the most prevalent except for the Forward, which I did not tabulate.

Varying periods of courtship displays precede pairing. The male alone performs these displays; or if the female also performs them, she usually does so after pairing and often displays with less intensity and frequency than the male. Displaying males may remain in the colony in the morning, but more often leave to feed, then return. I noted several males that displayed several hours for three and four days before successfully pairing. And, judging from the fact that I noted males still displaying as the breeding colors waned, I assume that some males never pair. Although I have no data that allow me to estimate the percentage of displaying males that do not pair, my observations suggest that the percentage is small. While some males succeed in pairing only after several days of displaying, for many the pairing occurs within one hour after returning to the colony. Some males submit much more quickly than others to the pairing attempts by females.

Pair-formation

Once a male begins to manifest his repertoire of displays, females soon appear, flying to perch on nearby branches. These potential mates assume an alert posture with sleeked plumage, watching the male's performance. I counted as many as ten females in the vicinity of a displaying male. The site where the male displays becomes a territory in the sense that he defends it vigorously against all comers. The area is usually a horizontal branch or an empty nest, if available. Later these nests usually become their own. Sometimes the aggressiveness, shown by the displaying male and the various females intent upon pairing, is so vigorous that their activity totally destroys the appropriated nest. If an unoccupied nest becomes the display site and territory, the male defends little more than the nest itself. However, I observed one male that, during one afternoon, defended two vacant nests about two feet apart. Another male defended, for part of an afternoon, two nests between four and five feet apart. If the site for display is a horizontal branch, a male that has not mated will chase off other birds along a four to six-foot length, infrequently more or less. Once the bird has mated, however, the aggressive tendencies for defending an area much beyond the reach of the bill wane.

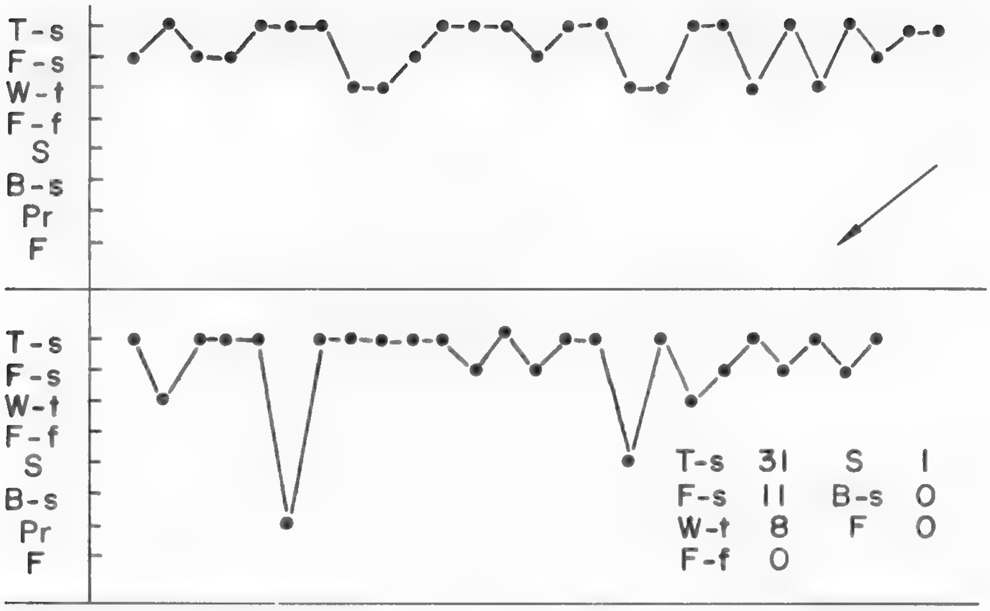
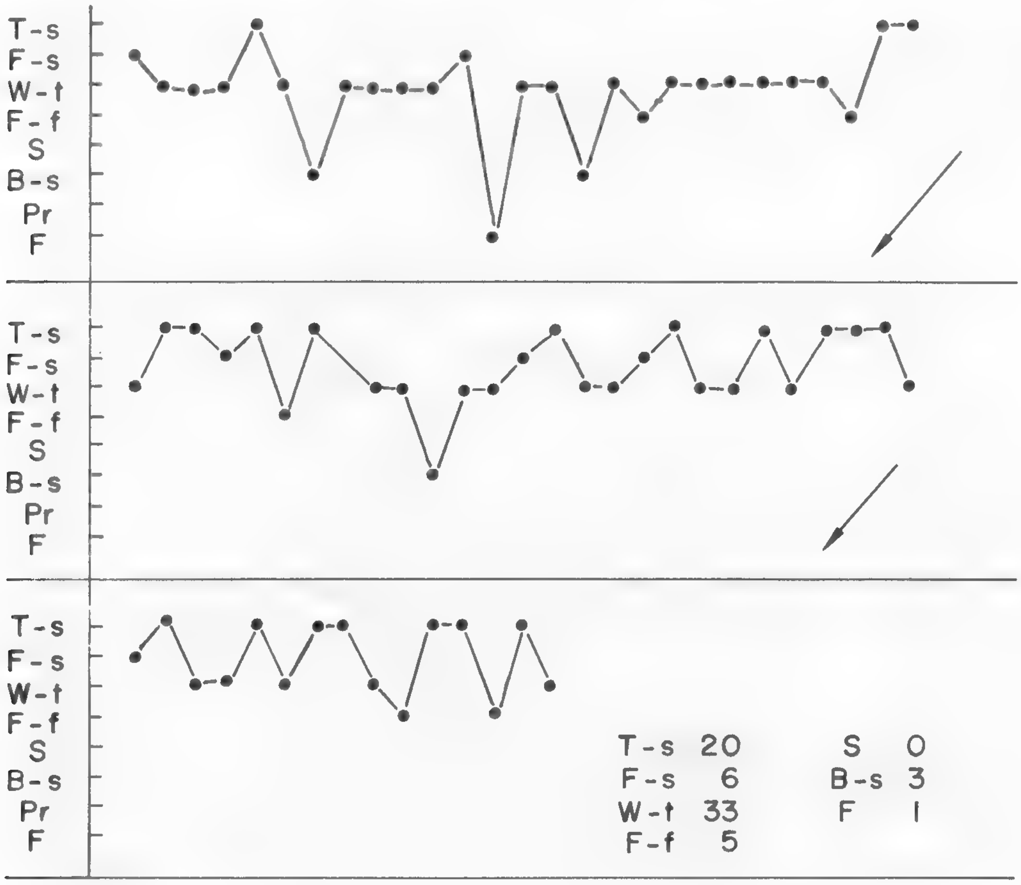


Figure 5. The sequence and frequency of displays given by an unpaired male during a ten-minute period (16:50–17:00). The letters signify the following displays and activities: T-s, Twig-shake; F-s, Forward-snap; W-t, Wing-touch; F-f, Flap-flight; S, Stretch; B-s, Body-shake; Pr, Preening; F, Forward. The numbers indicate the total displays given during the ten-minute period. Figures 6 and 7 show similar data for three other ten-minute periods. Table 1 tabulates the total number of displays during a 220-minute period.

Figure 6. The sequence and frequency of displays given by an unpaired male (same bird as in Figures 5 and 7) during a ten-minute period (14:19–14:29).



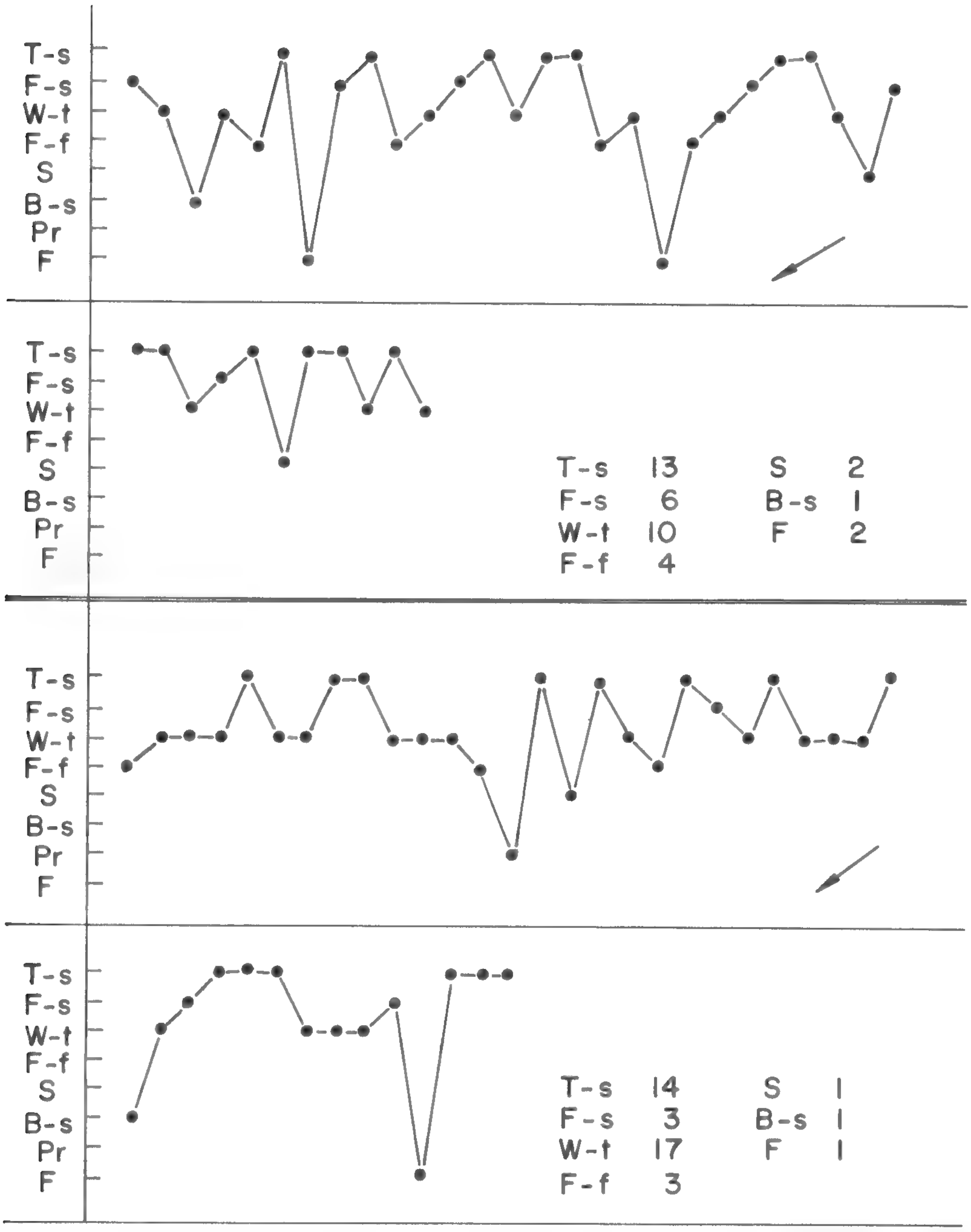


Figure 7. The sequence and frequency of displays given by an unpaired male (same bird as in Figures 5 and 6) during two ten-minute periods: 16:09–16:19 (top) and 14:40–14:50 (bottom).

Pair-formation involves sufficient aggressiveness on the part of the female to overcome the male's aggressive behavior. Although his actions indicate his readiness to breed, he attacks all males and females that come near, often repeatedly driving off four to six or more different females in a period of one to four hours, or for several days, before one or several females finally succeed in establishing a pair-bond. The latter is accomplished when a female flies to a male and, surprising him from behind, lands on his back and succeeds in remaining there long enough to subdue his aggression through repeated blows on the head. Males often rotate on a branch to face in the opposite direction when giving a Forward. This is one of the times when females often fly to the male's back. Interested females standing on nearby perches show no aggressive tendencies while the male displays. They maintain a sleeked plumage as they watch him and as they fly to approach him. Just before landing upon his back, however, the female erects her crown and neck feathers. Only once did I record a female with sleeked plumage landing on a male. He immediately dislodged her. A frontal approach never succeeded, and the females invariably veered away when faced with the male's aggressive posturing. Landing beside a male likewise rarely led to pairing. Males sometimes flew up from their perch to attack an incoming female head-on. Both birds fluttered to the ground, fighting. Within several minutes, often less, the male returned to his perch and resumed displaying. Almost all successful matings occur when a female lands upon the male's back; for then he has difficulty striking at her. Even so, only a fraction of the back-landings prove successful in pairing. The movements of the male usually dislodge the female and force her to flee. She, of course, strives to retain her advantageous position while striking vigorously at his head. A male, unable to dislodge the female, soon crouches and submits. She remains standing on the male's back for some time, often several minutes, rubbing her bill against the side of the male's neck and face, nibbling his crown, and sometimes gently grasping the neck or head with her bill.

The male, crouched in the nest with a female on his back, eventually ceases in his attempts to fight back. His feathers remain erect, however, and the female, after remaining there from some seconds to one or two minutes, dismounts. The female then turns her aggression toward any other female that attempts to mate with the male she has just subdued. Sometimes, the male's submissiveness does not stop the female's aggressiveness. In that case the male struggles to rise and either attacks the female or flies off. He soon returns, however, usually attacking the female and driving her off. Occasionally, though, the pair engages in mutual Back-biting, a common behavior shown by the pair when greeting (discussed below).

Polygamous Bonds

One female, then another, makes forays to the displaying male. Some veer off. Others attack. Frequently, two females land on the male almost simultaneously, quickly subduing him. If the two females overcome their aggressiveness toward each other, which they frequently do, then a polygamous pair-bond is formed. I saw dozens of these trios, two females and one male. Some of these bonds were tenuous and lasted only about 30 minutes, others continued for several hours, and still others remained intact after several days. Most trios dissolve before the egg-laying period, probably because one female invariably forms a stronger bond, forcing the departure of the other. The one exception I noted occurred in a nest under continual observation, in which I saw a trio and one egg. Four days later a female sat on three eggs while another female stood above the nest on a perch. The male flew in with nesting material twice during the afternoon, and each time the three birds displayed. All three had yellow soft parts at the time. The following day I saw only two egrets at this nest.

At times as many as three females may fight one another and the male at the male's display site. I never witnessed any successful pairing involving more than two females although, for nine minutes, four birds with red bills remained side by side amiably in a nest with four eggs that they had taken over from an incubating pair. Also, an apparently monogamous mating sometimes becomes a temporarily polygamous one. One of several red-billed females, after making a number of passes at a displaying male, may succeed in pairing with a male. If successful, the female must often contend with other females still desiring to mate at this time. She may now direct her aggressiveness toward one or more of the females that continue to make flying passes at the pair. I often witnessed a second female making a successful entry minutes after a previous female had seemingly succeeded in pairing. The second female, when successful, was able to keep one foot on the back of both the male and female, and strike at them, keeping them subdued for a time. Finally, all three birds displayed and a polygamous bond was established. Sometimes one sees a "totem pole" including three birds, the male on the bottom supporting two females, one standing on the back of the other.

Post-pairing Behavior

Back-biting Display.—This display appears only between mated birds. Typically, the male and female performing this display stand side by side, facing in opposite directions. They simultaneously nibble the feathers of each other's back with a quivering horizontal head motion and with a series of rapid open-close movements of the bill. They partially raise the crest and erect and spread the plumes of the back. This display occurs most frequently during the initial period after pairing when the two birds remain at the site for long intervals, often for several hours, and engage in mutual displays, of which Back-biting is the most prevalent. Once incubation commences, however, this display diminishes in frequency partly because the sexes now spend longer periods apart, one bird incubating while the other feeds away from the colony. Back-biting during the incubation period takes place primarily at the time of nest-relief.

Copulation.—Copulation may or may not occur immediately after the initial displays that assist in establishing the pair bond. In fact, when the male rises, after having been subdued by the female, both birds engage in mutual Back-biting for the first time. The male, continuing to Twig-shake, occasionally gives a Stretch that leads to a mounting of the male by the female. In fact, in the early stages of pairing, the female often mounts the male a number of times before the male mounts his mate for the first time. I saw a male mount his mate within three minutes after the initial pair-formation. I also observed a male mount and copulate for the first time a full hour after the first Back-biting.

During copulation the female sits on the tarsi, keeps her head withdrawn or partially outstretched and tilts her bill slightly upward. She moves the wings away from the body, forming a wider platform on which the male can more easily maintain his balance while treading. The plumages of both sexes are compressed throughout copulation although I once saw the male's crown partially erected. The male mounts from the side or rear, and facing forward, treads—first slowly, then more rapidly, crouching as the intensity of the treading increases. As the male begins to tread on the female's back, he often retracts his head and neck, but soon extends his bill to touch the female's crown. Although the male neither gapes nor nibbles the female's plumage during some copulations, many copulations are accompanied by nibbling or grasping the female's crown, nape, or neck. Finally, the male depresses his tail and moves it horizontally back and forth against the exposed cloacal region of the female, flapping his wings to maintain balance.

Copulation, before and during nest-building, often takes place after the female solicits with a Stretch, then crouches with gaping bill pointed diagonally upward. During incubation, however, the male often mounts and copulates without first displaying, and with no solicitation by the female.

Paired egrets almost always copulate in the nest or at, or near, the site that the future nest will occupy. I recorded a few exceptions to this: A pair that had recently completed building a nest copulated on a branch several feet away. On another occasion, a yellow-billed bird ascended to an empty nest several feet above its own, where it displayed and copulated with an egret, presumably its mate, that flew into the nest. The female then descended to her own nest with a bamboo twig in her bill; the male flew off. And again, a red-billed pair copulated in an empty nest about six feet from its own platform. After one bird flew off, the other returned to its nest.

Postcopulatory Behavior.—Postcopulatory behavior varies, depending in part upon the stage of the breeding cycle. Rarely, one egret may strike its mate; if this occurs at all, it happens after the first copulation of a newly mated pair when other females, still interested in the male, are attempting to establish a pair bond. Then the male and female may strike out at the intruder, and the male's aggression may be so roused that he also attacks the bird with which he just copulated. The postcopulatory behavior of the male may involve one or more Twig-shakes if the pair-bond has only recently been established. Fluffing out and shaking the plumage (Body-shakes), followed by bouts of preening, constitute common postcopulatory behavior in both sexes. Sometimes the preening is omitted; more rarely, a male or female may not Body-shake following copulation. If the birds copulate in their nest, they frequently engage in nest-building behavior immediately following copulation. Back-biting sometimes follows dismounting by the male, at least in the early stages of the breeding cycle.

Instability of Some Pair-bonds

In spite of the aggression shown during pair-formation and the subsequent displays and frequent copulations, the fact that polygamous bonding—though temporary—occurs, that some promiscuity was noted, and that attempted rapes and occasional changes of mates take place, shows a certain fragility of many pair-bonds. Mountfort (1958) mentions an incident in southern Spain in which a male Cattle Egret copulated with three different females in "quick succession."

I saw a number of attempted rapes by mated and unmated males with paired females, but I saw only one that succeeded. In this instance a female watched her mate fly to the back of a female in an adjacent nest only a few feet away. He succeeded in keeping the mounted female down and copulated with her. Immediately afterward the female turned her head and struck at the male as he flew back to his mate. Within one minute the mate of the raped female returned. After a few seconds of mutual display, the two pairs sparred back and forth. In this case I may have witnessed birds that had recently maintained a polygamous bond. The nests of both were partially built, and both pairs had orange bills. In another case, one male stood on a nearby branch and made no attempt to drive off an intruding male that tried to rape his mate in the nest. Instead, he directed his aggression toward a neighboring nest. The female and the unsolicited male fought, fluttering to the ground. The female returned and engaged in Back-biting with her mate.

In an apparent change of mates, a red-billed female flew into a newly constructed nest containing a red-billed pair that had been standing quietly together, and that probably had mated a day or two previously. The attacking female was driven off once, then again. After a sharp exchange of blows the female succeeded in her third attempt and drove the mated female off the nest. The male attacked the second female much less vigorously than his mate had. The new female gained a position on the male's back and struck at his head, subduing him within seconds. She dismounted. As she nibbled the feathers of the male's back, he displayed with a Stretch. Both egrets began preening. The male's previous mate made no attempt to re-establish the bond.

An initial copulation following mutual displays does not ensure a successful pair-formation. I observed a number of instances in which a male attacked and drove his female out of the nest within minutes after they copulated. One female subdued the same male six times in a two-hour period. Each time, the pair displayed with Back-biting. The male flew down to the ground four times, and each time attacked the female upon returning to the nest. He also turned on the female twice while standing with her in the nest.

Greeting Behavior

After pairing, the egrets' activities depend upon whether they must build a nest, or whether they have acquired one already intact. Mutual displays that strengthen the pair-bond occur frequently during the period following pair-formation, but decline gradually as incubation proceeds. These displays include Back-biting, Flap-flights, Stretches, Forwards, and *Rick-racks* — the latter being the call rendered by both sexes during greeting ceremonies at the nest. All of these displays, except the Flap-flight, may be part of a greeting ceremony.

Aside from Back-biting, newly paired birds most commonly performed the Stretch, which appeared in 73 per cent of one hundred greeting displays I recorded, and always preceded Back-biting. In greeting ceremonies at the nest, the time spent in display and the frequency of both Back-biting and Stretch decreased as the time of hatching drew nearer. The Stretch often ceased altogether midway in incubation, at which time greetings at the nest frequently involved no more than low intensity Back-biting and rarely not even that. *Rick-rack* calls, however, always marked greeting ceremonies at the time of nest-relief. Forwards and Flap-flights disappeared usually by the time incubation began. The Flap-flight, common before pairing as a series of flights to and from a nearby branch, occurred after pairing predominantly as circle flights.

After pairing, and throughout most of the incubation period, the incoming male frequently lands on the back of the sitting female at the nest. After vocalizations and some nibbling of the plumage the bird usually dismounts, and both birds may then Back-bite. I have seen males enter the colony, land on the females' back, tread, and copulate before dismounting. I did not see back-landings when the nest contained young; nor can I state whether or not the female lands on the male's back during incubation although she does so, at times, into the early nest-building period. The majority of birds entering the colony fly directly to, and land in, their nests. Sometimes, however, birds land several feet outside the nest and walk to it. Many nests, because of their location on a tall bamboo, or because of the density of other nests in the immediate vicinity, allow the proprietor no option of landing elsewhere than on the nest.

Even when the returning male or female lands a short distance outside the nest, the greeting behavior usually occurs within the nest. However, I have noticed the in-nest bird, on leaving, exchange Stretches and Back-bitings with its mate outside the nest.

If the birds have begun to build, the greeting ceremonies often involve Twig-passing. Even well into the incubation period, one parent may appear at the nest after a long absence with a bamboo twig in its bill and pass it to its mate. Sometimes, no greeting ceremony marks nest-relief during incubation. One member of a pair may enter the nest, and its mate leave without any overt display other than low-intensity *Rick-racks.*

Territory and Nest Sites

An unmated, red-billed male enters the colony and selects a site on, or near, which he and his future mate will build the nest. The site may be on a horizontal branch of a bamboo stalk, in a tall *Ceiba* tree, or on a tall bush growing among the bamboo. The top portion of a fallen bamboo, if it is elevated and more or less parallel to the ground, serves as a favorite site for displaying males. Such horizontal poles are frequently unsuitable for nesting sites, however, because the side branches often extend up or down and therefore provide no fork to support a stable nest. In such cases the male defends a portion of the horizontal bamboo pole until pair-formation occurs. Then the pair construct a nest at a site close by—often only several feet, and seldom more than several yards, away.

The best example I observed of a horizontal bamboo pole defended by several birds was that of five red-billed males that displayed, defended, and paired on the same four-foot stretch of bamboo at different times between 15 January and 17 February.

Male Number 81, 15 January–17 January
Male Number 72, 21 January–24 January
Male Number ?, 25 January–3 February
Male Number 47, 3 February–13 February
Male Number 46, 15 February–17 February

All paired successfully and nested within three feet of the bamboo. Once each had selected a site for his nest, that spot became the focal point, and the bamboo no longer functioned as a territory. Judging from the proximity of several other nests to this bamboo stalk, two other males (Numbers 74 and 80) very likely defended this site prior to pair-formation.

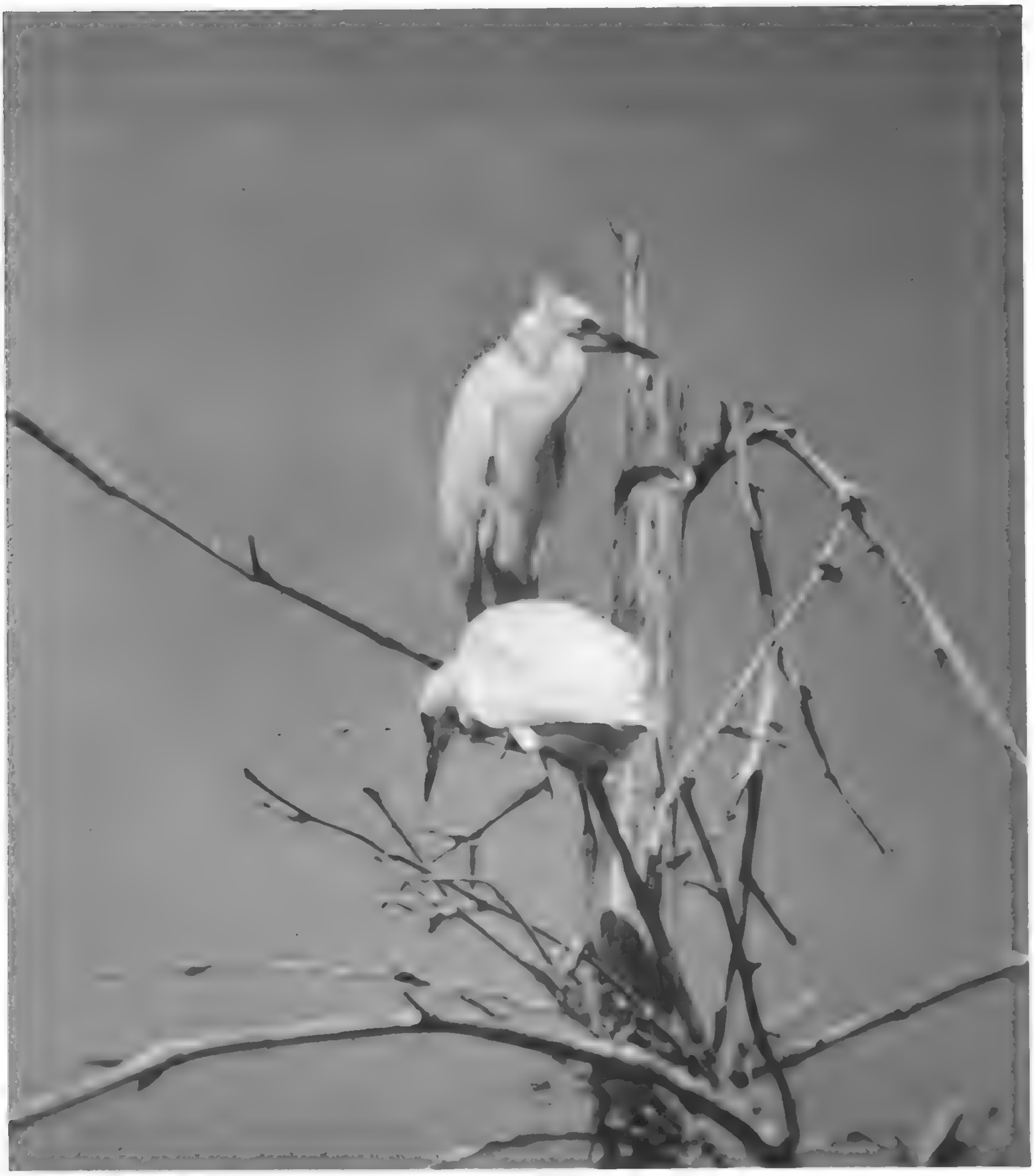


Figure 8. Two full-grown immatures with dusky bill and legs, and pale yellow lores and irises, stand above their nest. The wind blowing from the left of the photograph caused the feathers on the occiput of one bird to ruffle into a temporary crest.

The size of the defended site varies with two factors: the physical nature of the site where the male displays, and the stage of the breeding cycle. A male, selecting a site at the edge of a bush or on a small lateral branch of bamboo, can manifest territoriality to the extended reach of its bill in any direction. Egrets selecting larger branches of bamboo may drive off birds along a given length usually from three to six feet, sometimes more. When nest-building begins, the nest alone becomes the territory. An established pair may prolong the nest-building efforts of an adjacent pair with Forwards, but seldom is a newly mated pair deterred from nesting at a chosen site by incubating or brooding egrets. Nests only eight to 10 inches apart are not uncommon. I found several nests in which the sticks of both made a continuous platform, and in which the bodies of the incubating parents touched one another as they sat on their eggs.

Although a pair's territory encompasses the nest and the extent to which it can reach with its bill, it may temporarily extend beyond — to a neighboring nest that has been abandoned. Intruders, attempting to take over an empty nest or to steal nest material from it, often encounter threatening Forwards from an adult in an occupied nest next to the abandoned one. The incubating egret sometimes enters the vacated nest, chasing off strange birds. It may defend the empty nest for a day — seldom longer, partly because vacated nests seldom stay unappropriated for long. An aggressive male establishes a territory in an empty nest, or a number of nest-building egrets use the twigs for their own nests.

On several occasions, I watched a mated pair appropriate a vacated nest and, noting an adjacent nest also empty, establish a territory that included both nests. For several days the pair moved back and forth, building, displaying, and vigorously defending both sites, until a more aggressive pair of egrets took over one of them or until the first pair commenced egg-laying. One pair defended three nests for a day, then settled in one of them. Another pair, trying to defend three nests, lost them all to more aggressive birds.

Nest Construction

Cattle Egrets in the colony demonstrated considerable flexibility in the selection of materials for building nests. Generally, they used dead bamboo twigs. Late nesters, unable to find a sufficient quantity of twigs close at hand, resorted to stems of dead grass or pieces of live vines.

Birds readily pilfered materials from abandoned nests or even those temporarily vacated by owners seeking food or nesting material. A twig, projecting several inches beyond the outer rim of a nest, may tempt the owner of an adjacent nest to pull it out and incorporate it into its own nest even under the eye of an incubating adult. Considerable pilferage occurs during nest-building. Any bird working with a long twig or piece of grass may lose it, especially if one end comes within reach of a bird in a neighboring nest. The latter invariably tries, and sometimes succeeds, in pulling the twig or grass free and then building it into its own nest. A tug-of-war over a piece of nest material may last for minutes. I watched, on several occasions, three birds pulling on a single stem of grass or a long twig. Three times in one afternoon, a particularly aggressive male prolonged the nest-building efforts of a newly mated pair by flying from its own nest, about 20 feet away, and grabbing in flight the twig or grass from the bill of a bird that had just returned to its mate. At two different sites, incubating birds rose and challenged egrets entering adjacent areas to pilfer material from abandoned nests. The defenders chased off the intruders, picked up bamboo twigs, and returned to insert them in their own nests. Sometimes an incubating bird must defend its nest against a neighbor or an outsider attempting to remove a twig projecting from the bottom of the nest.

Not all egrets show equal efficiency when building. Some, probably birds building for the first time, select sites too poor to support a stable nest and, unable to complete them, abandon the site; or they may complete the nest, lay the eggs, and incubate them for some time before the nest collapses or the contents fall out as they attempt to make repairs.

The Tremble-shove behavior by which sticks are placed in the nest includes a series of quick, short-amplitude, sideways head movements, and, at the same time, a downward movement of the bill, either forward or to one side. The bird holds the piece of nest material so that both ends of the stick project laterally, but often the bill grasps it close to one end. It places one end of the twig into the nest with head-shaking movements. With one end secure, the bird then grabs the opposite end and inserts it into the nest in the same manner. If the twig fails to gain a footing, the bird withdraws it and tries again.

The Twig-shake of courtship behavior resembles the Tremble-shove of nest-building and undoubtedly is derived from it. The Tremble-shove continues throughout the incubation and nestling periods, even when the bird brings no nest material and undertakes no nest construction. Both male and female regularly grab a firmly placed twig in the nest and Tremble-shove. This activity occurs most commonly in birds shifting positions during incubation, rising to leave after incubating, or returning to the nest. Of the three, birds rising to leave the nest Tremble-shove the least.

The female does most of the building; the male brings in most of the nest material. They occasionally reverse these roles, as occurred when one pair started building at a site next to an abandoned nest. The female spent a full hour in that nest pulling out twigs and passing them to the male as he Tremble-shoved them into the nest. Once pairing is complete and the nest is under construction, one bird of the pair is at the nest site at all times until the young are about eight days old.

For nests constructed on good sites, building may continue intermittently for three to six days. Some nests were nearly complete in two days; others appeared to be less than complete after six days. I did not measure the actual daily periods of time that individuals spent gathering nest material and incorporating it into the nest; but I know it varied greatly between pairs. I suspect that younger birds show less aptitude for selecting the best sites, are less adept at constructing a nest, and often fail to complete a poorly built nest in an insecure place. Consequently, they take more time than more experienced birds.

Nest-building may continue on and off through much of the incubation and nestling stages. On many occasions an incubating female rose to receive a twig from its mate. Spurts of nest-building occur most commonly during nest-relief when, in one hour, a male may make eight to 10, or more, successive trips for nest material even though there are well-developed young in the nest. Such bouts of nest-building behavior are usually opportunistic, probably depending on the discovery of a new source of twigs—usually an abandoned nest. Sometimes both parents, if they can pilfer material from a nest that is close by, bring in nest material and continue to build a nest that contains young over one week old.

Placing the first twig and the few subsequent twigs presents the greatest hurdle for building egrets. Using the Tremble-shove behavior, they lower the head with the lateral head-shaking movement until the twig makes contact with the branch of bamboo chosen for the nest site. The first twigs often fall the first time, but the birds grab them and try again. Frequently the twigs fall to the ground. A bird may position a twig a number of times before it is secure. After a day of building, sometimes only a dozen twigs are in place. From that point on, however, building proceeds more rapidly, if the male chose a good site.

While Twig-passing from male to female represents the usual behavior in building, I noted at a number of nests that incoming birds failed to relinquish the twig they carried. Their mates generally showed equal motivation for taking the twig. This resulted in a joint attempt at building with each bird Tremble-shoving the opposite end of the same twig. Such nest-building was largely self-defeating in that a single twig often occupied their attention for some minutes. Only when one bird finally surrendered the twig and showed no further interest in it, did the mate place it firmly in the nest. One pair showed considerable consistency in joint-building—working together on the same twig. Twig after twig, brought in by one bird, was simultaneously Tremble-shoved by both.

My impression about joint-building is that it occurs predominantly in birds nesting for the first time. It is impossible to be certain of this, however, without color marking birds of known age. An indication that first-nesters may be involved in much of the joint-building is that many of these birds constructed nests at poorly selected sites. Joint-building seemed to predominate in the earlier stages of nest construction although I recorded it in one pair that had a complete nest but no eggs.

One parent made eight to 10 trips from its nest to an abandoned one about 20 to 30 feet away, returning each time with a twig. As soon as the parent entered the nest, both chicks grabbed its bill, begging for food. The parent simply dropped the twig in the nest and flew off for another without a sign of Tremble-shove behavior or an attempt to incorporate the twig into the nest. I saw similar behavior in another nest that had neither eggs nor young.

Rarely, what seems to begin as a nest pilfering foray becomes one of nest destruction. I saw red-billed males that seemed to have no nest or mate move into an abandoned nest and pull the nest apart, dropping the twigs to the ground. On another occasion a yellow-billed bird methodically destroyed what was left of one of the many nests I had under observation, pulling out twigs and dropping them until the last twig was gone. Then the egret moved to another nest, only to be chased off before it could steal any twigs. It flew to a third nest, also empty, about 30 feet away. Again, an incubating bird on an adjacent nest gave a Forward, and the intruder left. Finally, at still another nest, the yellow-billed adult pulled out and dropped several twigs, and then, with a long, straight one in its bill, flew immediately to its own nest.

Incubation

Incubation, within a few days after commencing, develops a pattern whereby one bird, probably the female, sits most of the day and is relieved late in the afternoon. Little activity occurs at the site of an incubating bird. On warm days, and during the later stages of incubation, the birds spend considerable periods off the eggs but within the nest. Gular fluttering is evident as they assume a standing or crouching posture above the eggs with wings partially open and drooping, shading the eggs with their backs to the sun. Bouts of preening involve the greatest portion of non-incubating activity.

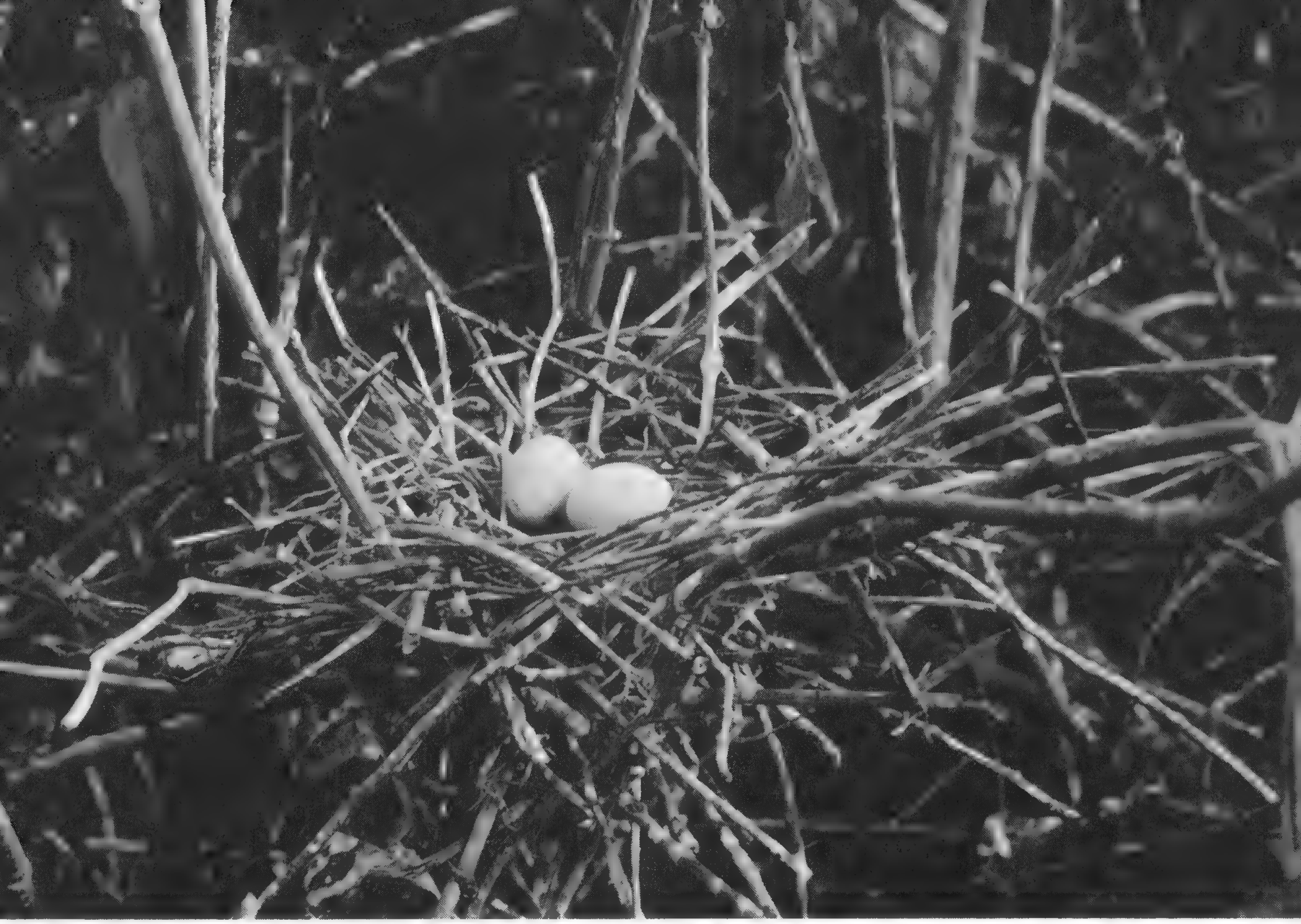


Figure 9. A typical Cattle Egret nest with two whitish eggs. This nest, and almost all the nests in the colony, were constructed of bamboo twigs.

Comparisons of Some Heron Displays

While preparing this manuscript on Cattle Egrets, Blaker (1969) published an excellent and rather detailed account of the behavior of this species in South Africa. I, therefore, purposefully omitted treating more fully some aspects of breeding behavior thoroughly covered by Blaker, especially as related to the cause and evolutionary origin of displays. His account represents the first detailed report of the Cattle Egret's behavior. Meyerriecks (*in* Palmer, 1962) studied this species in Florida.

My observations do not corroborate perfectly those of Blaker and Meyerriecks. I observed some things that they did not, and *vice versa.* Our interpretations of various behaviors, however, differ rarely.

Among agonistic displays the Forward appears throughout the annual cycle. Many displays given by an unmated male, and designed to attract females, contain components of this aggressive behavior. Meyerriecks (1960) discusses the interaction of sexual and hostile tendencies. I describe the Forward and Upright as the major aggressive displays. Meyerriecks (1960) discusses additional hostile displays that I have included with the Forward and Upright. Blaker (1969) likewise preferred to designate different intensities of hostile behavior as a manifestation of degrees of an agonistic display rather than separate displays. Blaker (1969) noted that resting or feeding Cattle Egrets performed the Supplanting-run only on the ground. I noted it frequently on the bamboo and bushes in the colony where it was used most often by incubating birds that moved to supplant a bird landing, or walking, too close to its nest.

The Forward, a hostile display in herons, contains a vertical tail movement referred to as Tail-flipping. I did not see this in Cattle Egrets; nor did Blaker, although Meyerriecks (1960) records it in nine other species of North American herons.

I cannot agree with Blaker that the Stretch "... is inconspicuous in comparison with other common displays in unmated males." Indeed, I believed it to be the most conspicuous of the non-aerial displays. On the other hand, we both found that unmated males performed fewer Stretches than most other displays. The Stretch assumes its importance in pair-bond maintenance during greeting ceremonies at the nest and in soliciting the male to copulate. While Blaker describes a fully appressed crest as a consistent component of the Stretch, I observed frequent Stretches with crest and neck feathers erected in males. Meyerriecks (*in* Palmer, 1962), watching these egrets in Florida, commented that the Stretch begins when the egret "... rapidly moves his legs up and down in a dancing motion. ..." Neither Blaker nor I recorded this for the African or South American Cattle Egrets.

Herons perform a variety of aerial displays in both a sexual and agonistic context: Pursuit, Nipping, Aerial-stretch, Flap-flight, Tumbling Flights. Cattle Egrets perform only the Flap-flights. Meyerriecks (1960) discusses the correlation of aerial displays with body size, noting that small herons display more frequently on the wing and have a greater repertoire of aerial displays than larger herons. The Cattle Egret provides an exception to this rule, since it is a small heron and exhibits only one aerial display, the Flap-flight. Many of the aerial displays performed by herons involve unmated males leaving a display site (territory) to chase single females. In the Colombian colony, unmated, displaying males rarely chased; rather they remained at their chosen site except for Flap-flights which never involved chases, although they frequently ended with supplantings.

Blaker noted that the Flap-flight in African birds was always a direct flight between two points. He never recorded any circle-flights. Although the Colombian egrets performed numerous straight Flap-flights, infrequent circle-flights took place both before and after pair-formation. In fact, the few Flap-flights after pairing are most likely to be circle-flights.

Blaker discusses differences between the Twig-shake of the Cattle Egret and the Forward-snap, or Snap, of other herons. The Twig-shake, while resembling the "down" position of the Snap, described by Meyerriecks (1960), manifests some cogent distinctions warranting a separate name for the display. Blaker apparently did not notice the Forward-snap in the African colony he studied. I recorded it as one of the common displays among unmated males. Females did not perform it. It appears to be homologous to the Snap described by Meyerriecks (1960) in North American herons.

The Wing-spread, as described by Blaker, I presumed to be the Forward. Blaker refers to the Wing-spread as the most characteristic display of an unmated male. I could not detect significant differences between Blaker's Wing-spread and the Forward, and therefore did not give it a different name. If there is a call accompanying this display I did not record it. Differences in calls may signify the difference between two agonistic displays that are similar in form—one serving primarily to maintain or increase individual distance, and the other functioning to reduce distance. Blaker describes two very distinct calls given with the Forward, a harsh "raa" and a soft, muffled "thonk," respectively. Thus, although the posturing and feather erection appear identical in the Wing-spread and the Forward, the call notes may justify the naming of two displays, since their accompanying calls effect different responses from other egrets.

Blaker believes that an interval of three or four days separates the establishment of a territory and the acquisition of a mate. In Florida these two steps in the breeding cycle are no longer than two to three days (Meyerriecks, *in* Palmer, 1962). This is rather short for most North American herons, which take longer than three days to form a pair-bond. In Colombia, Cattle Egrets varied greatly in forming pairs—from a matter of several hours to four days, or more.

The South African Cattle Egrets studied by Blaker usually abandoned their site within several hours of pairing, with the male flying off first, followed by the female. This I did not notice in Colombian birds. In the period immediately after pair-formation, as well as during nest-building, egg-laying, and incubation, one bird almost invariably remained at the nest. Even the nestlings had a constant guardian until at least one week of age.

The Green Heron engages in some nest-building prior to pairing. The Cattle Egret does not. A number of other herons may also do so, although information on this point is generally lacking.

The Wing-touch has not been described for any other heron except the Cattle Egret, in which I recorded the Wing-touch as one of the common displays in unmated males. Blaker (1969) suggests that it may easily be overlooked as a regular preening movement. I agree.

Summary

This paper reports the results of a study of the breeding behavior of the Cattle Egret (*Bubulcus ibis*) in a colony on the Cauca River near Cali, Colombia, from September 1968 to July 1969.

The soft parts change from yellow in the non-breeding adult to deep reds for about a two-week period at the beginning of the breeding season. Both sexes assume scarlet red irises, red legs, a red bill with yellow tip, and magenta lores. Buff- or salmon-colored plumes on the breast, back, and crest vary greatly among birds in the colony. Usually, the breeding colors change during the nest-building stage and, with few exceptions, have returned to yellow by the time eggs are laid. Both sexes typically show hostility with the Forward, Upright, and Supplanting-runs and by fighting. Pair-formation involves strong aggressive components of a number of displays shown by both sexes. The displays performed by an unmated male that has established a territory and advertises for a mate include the Stretch, Twig-shake, Wing-touch, Forward, Flap-flight, and Forward-snap.

Females move into the vicinity of an unmated, displaying male and attempt to pair by flying to his perch. All birds are driven off until an aggressive female succeeds in subduing the male's hostility by landing on his back and repeatedly striking at the head. Polygamous bonds with two females and one male are formed rather frequently, but do not last.

The pair-bond is maintained by both sexes performing some of the same displays shown by an unmated mate, especially the Stretch. In addition, they Back-bite and give the *Rick-rack,* a call always rendered during greeting ceremonies.

Males maintain a small territory of only a few square yards that shrinks after pairing to encompass little more than the nest. The female defends the nest with equal intensity.

Nest-building commences shortly after pairing. Cattle Egrets use twigs, mostly bamboo, and usually construct a nest in three to six days. Males bring in most of the nest material, and females do most of the building.

Acknowledgments

This study was undertaken while serving as a visiting professor at the Universidad del Valle in Cali, Colombia, with a grant given to Cornell University by the Rockefeller Foundation. To my colleague and friend, José Ignacio Borrero H., I am grateful for the help he gave me in innumerable ways, academic and otherwise; I also appreciate the generosity of Jesus Sierra, who kindly allowed us to study the Cattle Egret colony located on his property; and the help of Gerardo Cataño who cheerfully served as a field assistant when I needed his talents.

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THE BREEDING BEHAVIOR OF THE ROCK PTARMIGAN

S. D. MacDonald

All illustrations by the author unless indicated otherwise in their captions

All arctic birds seem to acquire a special beauty on their breeding ground, and once removed from it their plumage loses its brilliance and its evanescent vitality which is its characteristic. When we think of birds that are truly beautiful, few of us even consider the Rock Ptarmigan. Its basic white plumage of the cold months seems purely utilitarian, as does the drab, cryptically colored brown of the summer. To appreciate what a splendid creature the Rock Ptarmigan really is, one must see it in life in its arctic environment. The winter plumage, so flat and chalky white in museum skins, is vivid in the living bird. When the arctic sun is low, the delicate blues and pinks of the wind-sculptured snow impart to it an opalescent glow; against the blue of the sky or dark bare ground the ptarmigan can be dazzling white. The brown plumage against the tundra is truly a marvel of camouflage, and a simple description of the exquisite blending of soft, earth colors conveys a sterile image as compared with the bird in life.

Throughout the short arctic spring and summer the Rock Ptarmigan molts almost continuously and three distinct plumages are recognized (Salomonsen, 1950–1951). In early spring its immaculate whiteness matches the snow in the strong light of the arctic day. As the snow melts and extensive areas of bare ground appear, the appearance of patches of brown plumage on the bird keeps pace with the disappearance of the snow. Again, in autumn, the piebald plumage matches the piebald landscape; and as winter advances, the fresh white plumage, now flushed with pale pink, harmonizes with the new snow in the low light of the declining sun.

The Rock Ptarmigan (*Lagopus mutus*), a circumpolar grouse, is the most boreal of the three ptarmigan in Canada (Godfrey, 1966). There its breeding range extends to the edge of the Arctic Ocean. This paper deals with the life history and behavior of a high-arctic population on Bathurst Island, Northwest Territories, and is based on detailed field studies from 18 May to 15 August 1968 and during May and June 1969. The colleagues and students who assisted me either one or both summers were: David F. Parmelee, Philip Taylor, David Gray, Pierre Lamothe, and C. G. Hampson.

Habitat

At Bathurst Island in 1968, Rock Ptarmigan were widely scattered throughout suitable habitat with territorial males about one mile apart. The following year, with fewer birds in the same area, the males were separated by even greater distances. They select hillsides and ridges that have moist, hummocky tundra and well-vegetated depressions. These damp, plant-covered areas provide an ample food supply throughout the breeding season. Prominences in these areas and rocks on nearby ridges or at the edge of escarpments provide lookout posts for territorial males and necessary shelter from prevailing winds. During the first part of the breeding season the lives of territorial male Rock Ptarmigan are associated with these prominences where their activities make them conspicuous. On the other hand, females are always associated with depressions and lower areas where their cryptic plumage renders them practically invisible. When the breeding season is well advanced and when nests or young occupy the females, the males leave their prominent vantage points to molt, adopting the inconspicuous behavior of females in hummocky tundra.

Description of Display Structures

The colorful, or strikingly contrasting, secondary sexual characters that function as display structures in most species of grouse are not well developed in Rock Ptarmigan. They lack the brilliant neck decorations of prairie chickens (*Tympanuchus*), blue grouse (*Dendragapus*) and others; and their combs are less elaborate although no less brilliant.

Both male and female Rock Ptarmigan have combs, but the male's are much more prominent and brilliant (Figure 1). The combs, soft and fleshy, arise from a narrow featherless strip above the upper eyelid on each side of the head. The color of this tissue is pure red, and under various stimuli varies from a dilute red-orange to vermilion in the female and from vermilion to an incredibly vivid scarlet in the male. Both sexes can conceal or erect their combs and can enlarge them and intensify their color. In the female the tiny apterium or featherless area above each eye widens in a slight movement that can only be upward toward the mid-crown since the opposite would result in partly lowering the upper eyelid which does not appear to move. The color becomes more brilliant as the apterium is exposed, and its surface becomes slightly convex, textured, and more prominent, probably through engorgement of blood or lymph – perhaps both.

At the upper edge of the comb there is a small fringed flap which in the female appears as a single row of papillae less than a millimeter high. Even when the comb is fully exposed and the papillae are erect, the flap is not very noticeable. In a relaxed state it folds downward, and, along with the apterium, can be completely hidden by the plumage above the eye.

In the male the same components are larger and much more apparent, particularly during the courtship period when the whole structure is modified as a visual signal. A fully erected male comb can measure 20 mm long and 10 to 15 mm high. The erectile fringe of papillae may be 2 mm high and be single,

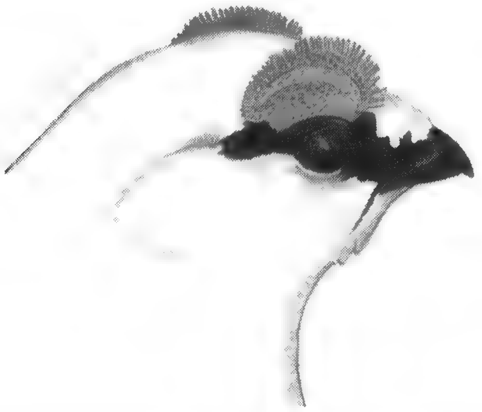


Figure 1. Adult male Rock Ptarmigan with combs fully erect. The color of the combs varies under different conditions from vermilion, when the bird is relaxed, to vivid scarlet, when the bird is excited. Note the papillae of the fringed edge and the textured surface. In a relaxed state the fringed portion folds down and the whole red area disappears beneath the crown feathers.

finger-like projections, or be bifurcate or tridentate. Usually all forms are present if the comb is intact, but some males lose portions of the fringe during fights, breaking the beautiful semicircle of the complete comb. Unlike the complex combs of other male grouse which are made up of sagittal rows, or densely packed papillae over the whole surface, forming a strongly convex contour curving prominently toward the midline of the crown, the combs of Rock Ptarmigan are almost flat. On the slightly convex surface directly above the eye there are many small surface irregularities giving a somewhat textured appearance. As in the female, the fringed portion of the comb folds downward, and the whole red area can be completely concealed by the crown feathers.

The presence of enlarged, vivid scarlet combs above a prominent black face mask serves to distinguish the male Rock Ptarmigan from the female. The combs achieve their greatest prominence in males after territorial activities begin; they are fully erect in all courtship patterns, including song-flights and aerial chases, and in all encounters with rival males except in aggressive confrontations of high intensity. The combs of females are most often exposed in situations of mild alarm, and in aggressive displays in defense of the nest or young. They seem to have little significance in courtship. In association with the male, the female conceals her combs. In cold weather, before active courting takes place, males may expose their combs briefly or incompletely during encounters with other males. While roosting or resting the combs are either completely hidden, or the fringe is folded down and covered by the crown feathers that move out laterally, protecting them from cold (Figures 2 and 3).

The size and color of the combs are apparently regulated by the presence of androgens in the male's blood (Salomonsen, 1950–1951; Watson, 1956). These hormones influence the bird's aggressive levels which in turn seem to reflect in the display activity, particularly in the height and frequency of song-flights.

The level of androgens in the males apparently declines by the time the females are incubating. Their combs then become less fleshy, smaller, and paler, and the papillae of the fringe are reduced. The upper portion of each papilla shrivels and seems to be sloughed off. The male, beginning to molt his

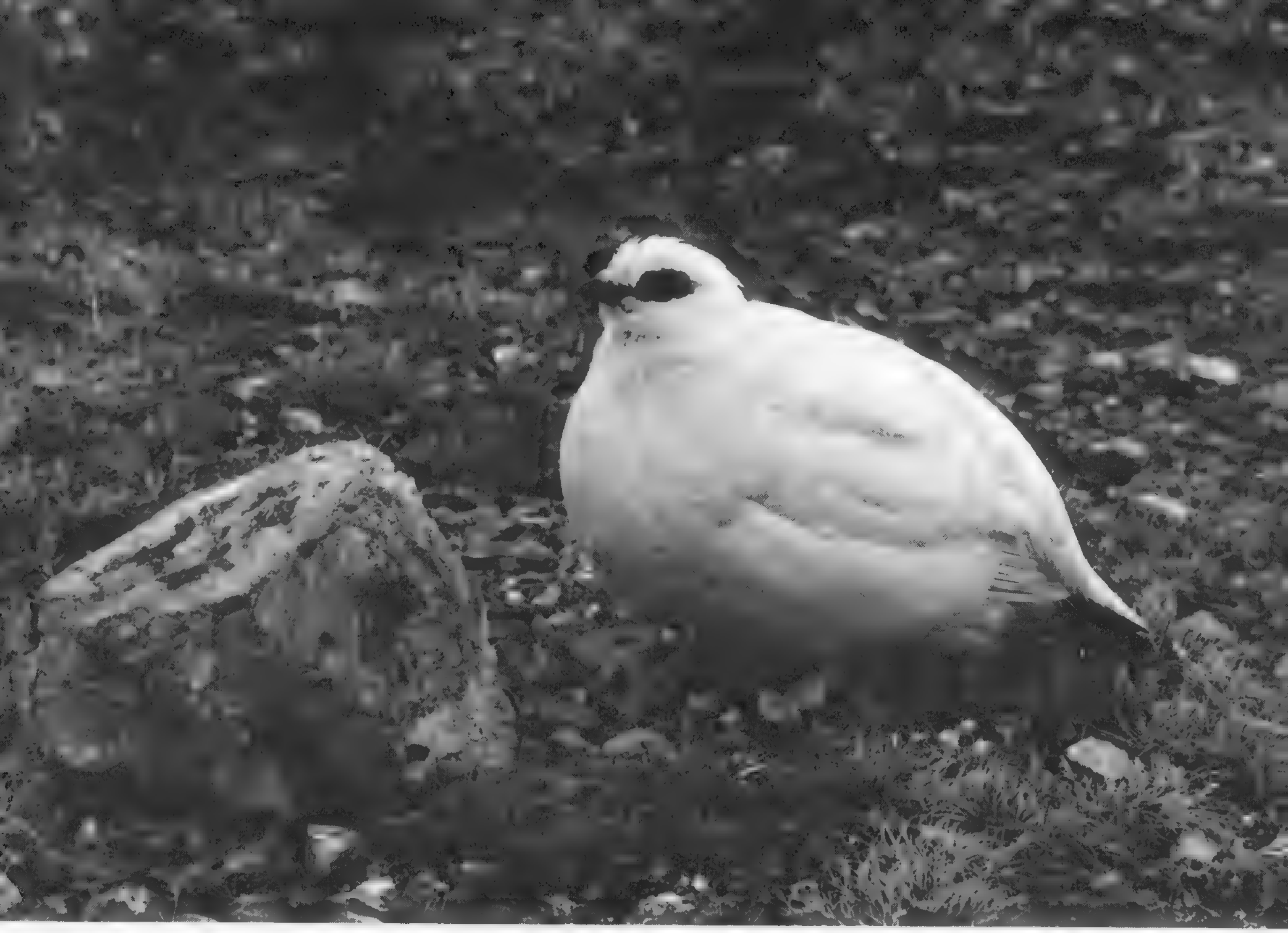
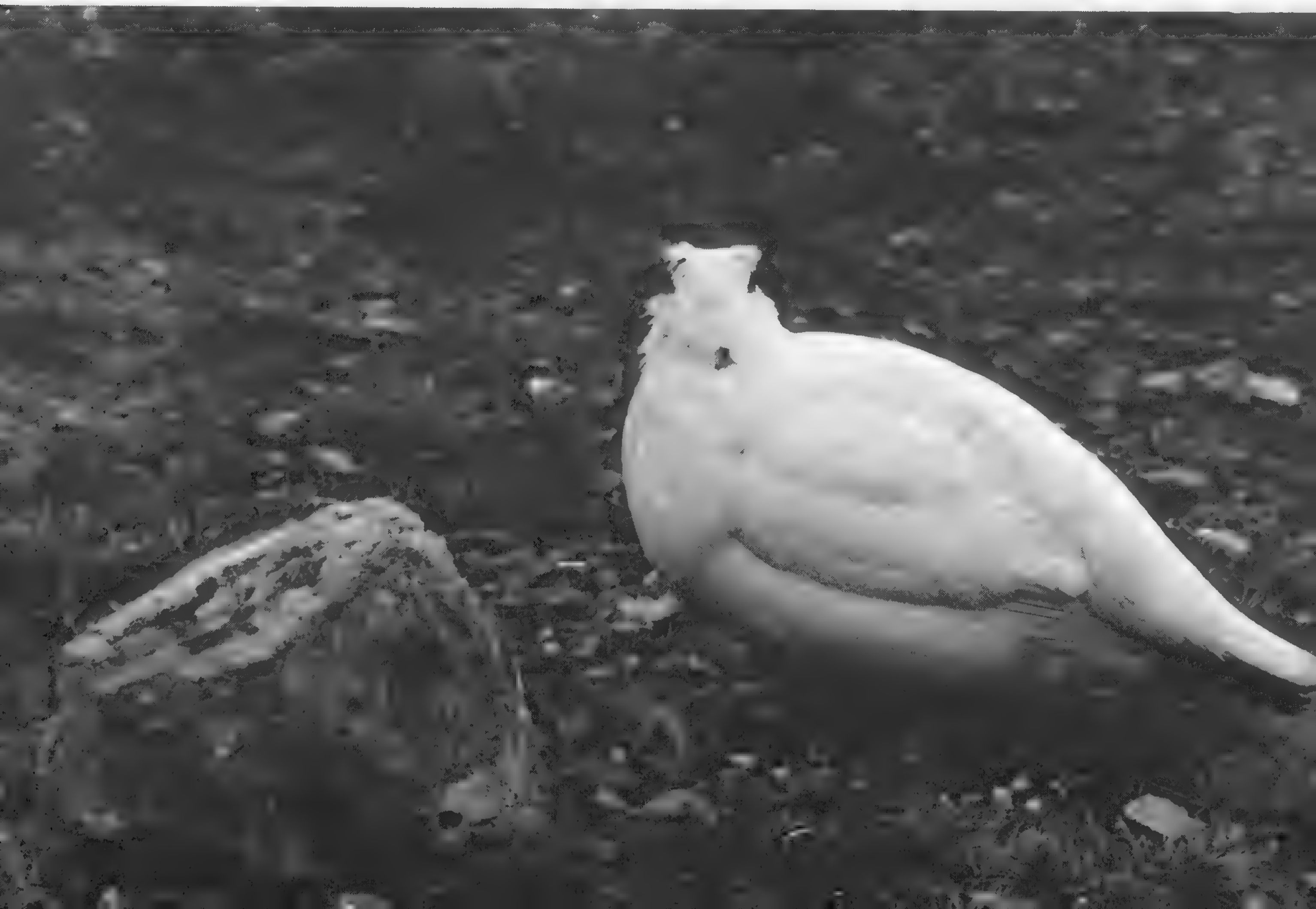


Figure 2 (*above*). A male sitting in the lee of a stone on the top of one of his lookout hummocks. The female was incubating about 300 yards away. An accumulation of droppings marked the lookouts. Usually the vegetation was better in these spots than in the surrounding area because of the added fertilizer.

Figure 3 (*below*). The male sheltering, as in Figure 2, and facing away from the camera. Note the crown feathers raised and spread laterally, protecting the partly inflated combs from the cold wind. The small patch of dark feathers on the nape may have replaced white ones lost in a fight.



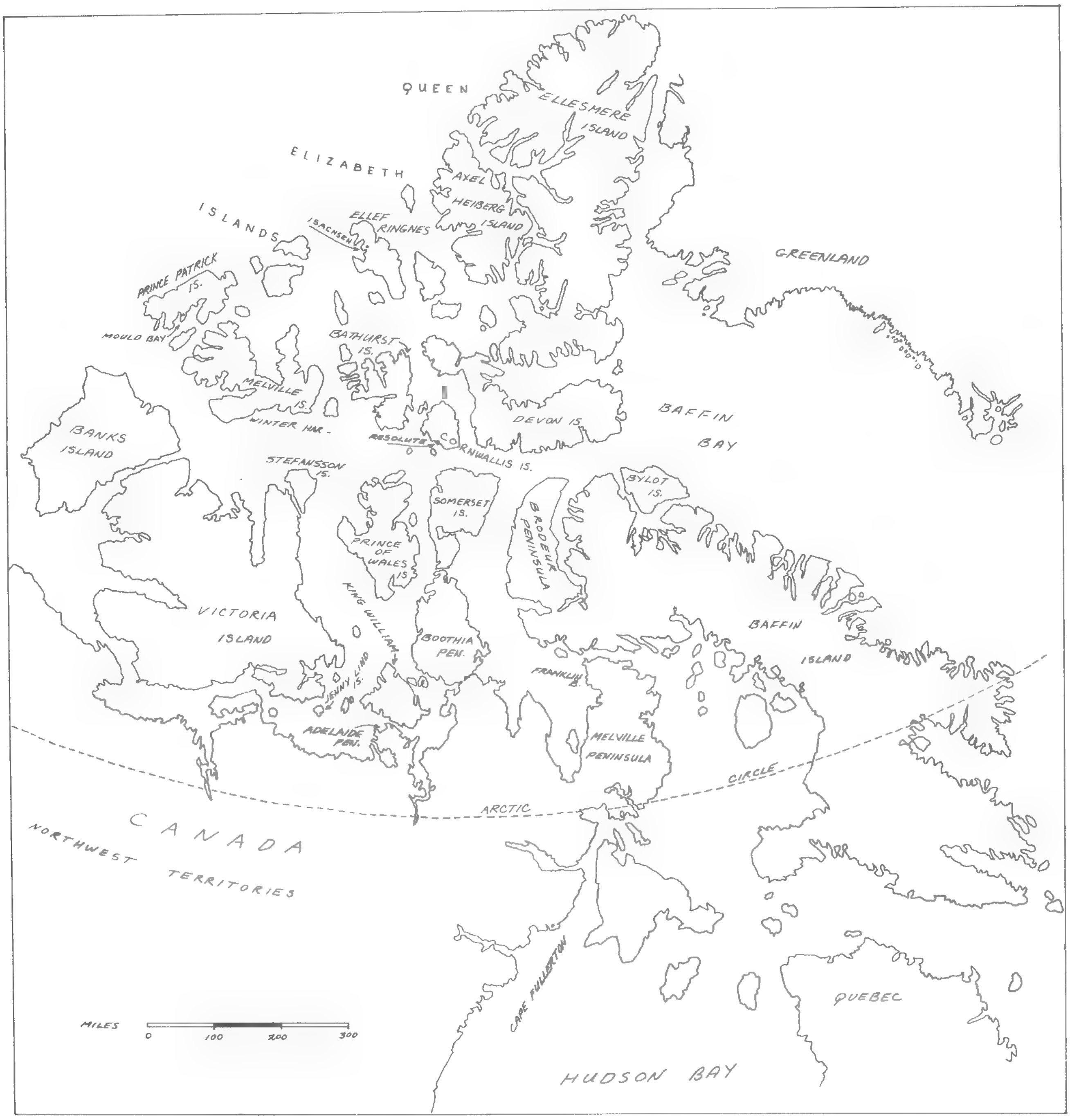


Figure 4. Map of Northwest territories, showing the location of Bathurst Island.

winter plumage now heavily stained by frequent dusting, becomes inconspicuous and moves to moist, well-vegetated hummocky tundra, frequently in gullies along small streams. At this time he gives the flight-songs only when disturbed and forced to fly, and the song pattern is incomplete.

Another structure, important in all display activities, is the black tail. The black face mask of the male is also significant, and to a lesser extent the blackish shafts of the flight feathers. The function of these pigmented areas is described in the sections on display.

Methods of Study

I presented the territorial birds with as many different stimuli as possible since, in a widely dispersed population, the detailed observation of some behaviors may be purely coincidental. Mounted male and female Rock Ptarmigan, set up in known territories, and appropriate vocalizations, recorded and played back, stimulated the living birds to respond accordingly. Replicas of

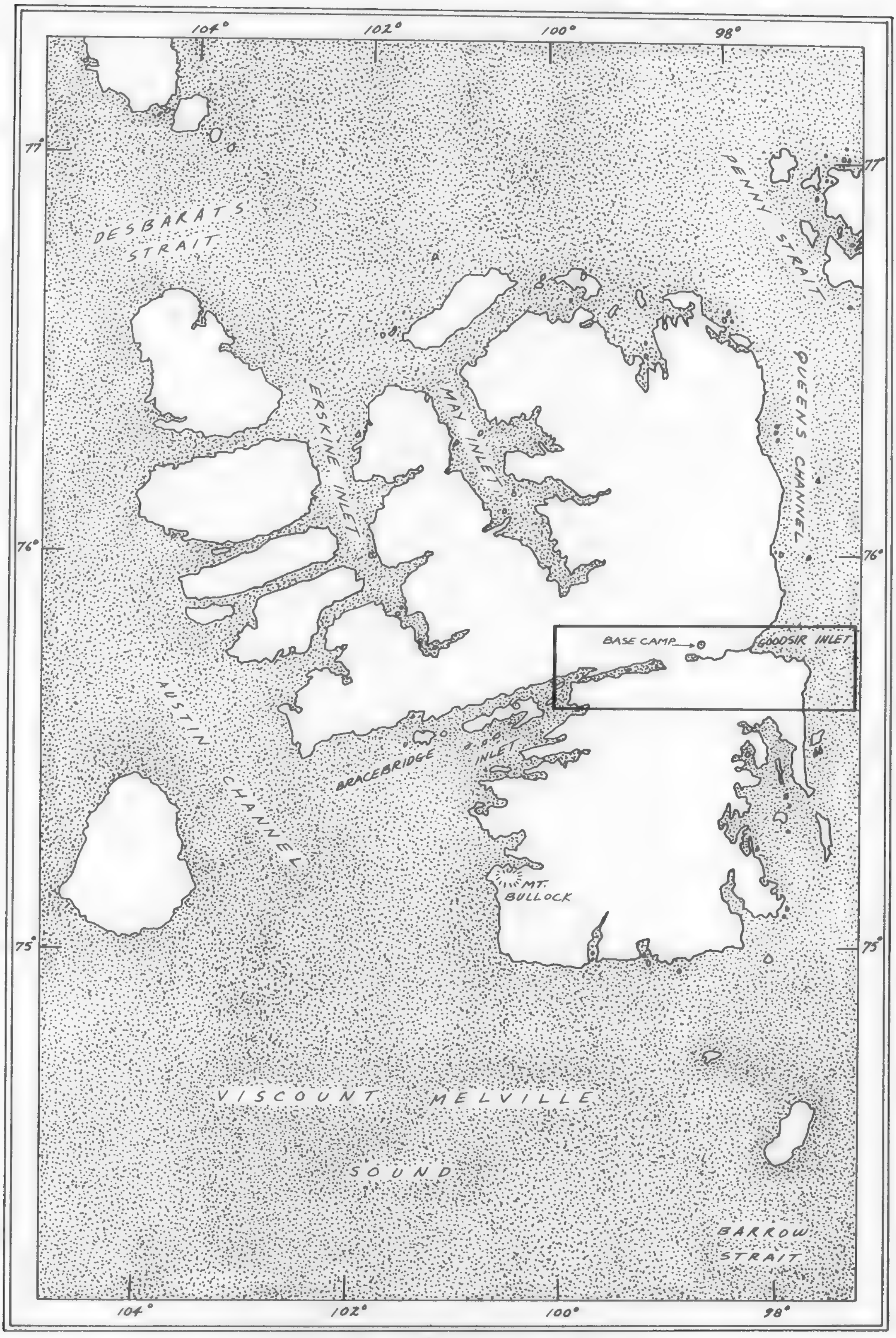


Figure 5. Map of Bathurst Island, showing the site of the study.

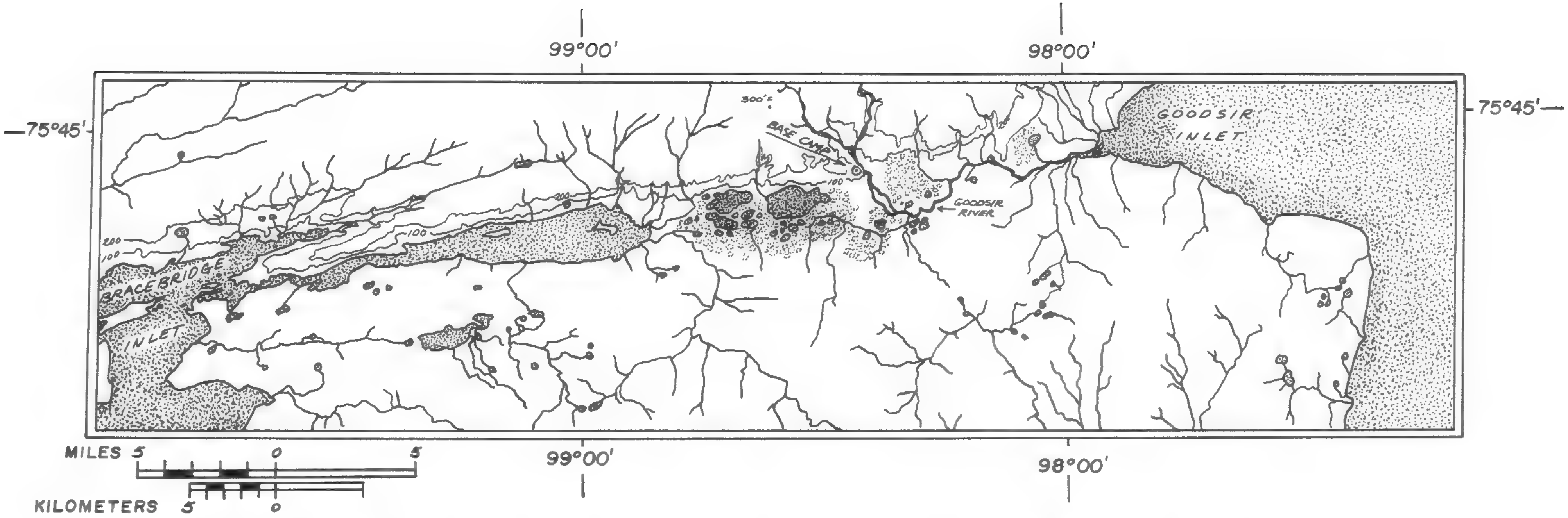


Figure 6. The research area on Bathurst Island, halfway between Goodsir and Bracebridge Inlets.

ptarmigan, made of snow, and crumpled white paper also attracted displaying males. Brown, patterned paper "feathers" were pinned to the white plumage of the mounted female specimen, simulating the "molt" to summer plumage. I attached red paper "combs" of various sizes to both male and female mounts and set them on bases that I hauled, at the end of a 100-foot string, like little sleds over the snow. Rock Ptarmigan usually became excited by the sudden appearance of these "new birds" in their territory, and making the mount move slightly intensified their reaction.

I decided that the best way to accumulate significant data on the ptarmigan was to observe them through binoculars continuously for many hours. At all times my assistant and I stayed so far away that the birds ignored our presence. During the period of constant daylight the watch extended throughout daytime and "nighttime" activity. The longest continuous observation was nine hours (06:00 to 15:38). Thus, by watching the female's activity until she returned to her nest to lay another egg, or to incubate, we found four nests.

We recorded vocalizations on 900-foot rolls of type LPM mylar base recording tape with a Uher 4000 Report-L, and a Uher 4200 Report Stereo tape recorder, and photographed displays with a Nikon F 35 mm camera, equipped with an electric drive, using a 135 mm *f* 3.5 lens and a 80-250 mm zoom *f* 3.8 lens.

Prenesting Behavior

Arrival.—Rock Ptarmigan arrive on their breeding grounds in the high Arctic very early in spring. Flocks occur on Fosheim Peninsula, Ellesmere Island, as early as April when the air temperature is still −40°F; females are present at that time; and some birds go about in pairs (Parmelee and MacDonald, 1960). MacMillan (1918) recorded them on 21 March in 1909, on the northern coast of Ellesmere Island (Figure 4).

We have no early arrival records for Bathurst Island (Figures 5 and 6); our records begin on 10 May. Evidence suggests that Rock Ptarmigan and shorebirds may reach their breeding grounds there at a somewhat later date than do the populations on Ellesmere Island (Parmelee and MacDonald, 1960). At Ellef Ringnes Island, more like Bathurst Island in climatic conditions, the first Rock Ptarmigan was seen on 30 May (MacDonald, 1959). These early arrivals are always males, as far as I have observed, but the females soon join them. They frequent the patches of bare ground swept free of snow by the winds, foraging for exposed plants of arctic willow (*Salix arctica*), *Dryas integrifolia*, and purple saxifrage (*Saxifraga oppositifolia*).

Feeding Behavior and Food.—While foraging, particularly if the weather is cold or windy, Rock Ptarmigan crouch so low that their breasts seem to rest upon their heavily feathered feet. They withdraw the neck toward the shoulders and fluff out the plumage, showing individual contour feathers. All movements associated with foraging, except the pecking movements of the head and neck, are slow and deliberate. They usually do not raise the head above the elevation of the back unless potential danger alerts them. The tail, with the black rectrices or flight feathers hidden by the long tail coverts, is kept below the horizontal level of the back and frequently brushes the snow. The minimal movements coupled with white plumage make the ptarmigan very inconspicuous against the snow-patched habitat. The pecking movements are very rapid and brief. When a twig of arctic willow is exposed, either by the wind or by the birds themselves, they remove the buds and smallest twigs with the tip of the bill and a quick sideways turn of the head. This lightning-like movement bends the twig at a sharp angle against the cutting edge of the bill and breaks it off with an audible snap.

Before the spring melt has advanced enough to promote succulent new growth, the Rock Ptarmigan depend mainly upon arctic willow twigs and buds, purple saxifrage buds, and buds and leaves of *Dryas*. During the period of vegetative growth and seed production, Rock Ptarmigan shift their preference to this succulent fresh food, including leaves, flowers, and seed capsules of a variety of plants. They seek the bulbils of *Saxifraga cernua* and, to a lesser extent, those of knotweed (*Polygonum viviparum*) and immature catkins of willows. Kuc (1964) determined, from 60 specimens of excrement collected in SW Spitsbergen, that mosses provided 3 per cent, horsetails 3 to 5 per cent, and angiosperms 95 per cent of the total bulk.

Parmelee *et al.* (1967) examined the crop contents of seven males and two females, collected during 12–23 May, and found that 60 per cent consisted of buds and twigs of willows (probably *Salix arctica*); 32 per cent of leaves and twigs of *Dryas*; 5 per cent of branch ends of purple saxifrage; 3 per cent of leaves, scapes, and seed pods of *Draba* sp; and some willow leaf galls. The summer crop contents of all immature ptarmigan that I examined in 1952 consisted largely of the leaves and red bulbils of *S. cernua*, with some insects, insect larvae, and spiders (MacDonald, 1952). The crop contents of four adult ptarmigan taken on 15 September consisted of: *Saxifraga caespitosa* (capsules and fruiting heads), 75 per cent; *S. oppositifolia* (capsules), 8 per cent; *Salix artica* (buds and small twigs), 8 per cent; *Papaver radicatum* (unripe capsules), 7 per cent; *Draba bellii* (unripe pods), 2 per cent; *Stellaria longipes* (a few leaves and one flower); *Ranunculus sulphureus* (1 fruiting head); *Saxifraga cernua* (1 leaf).

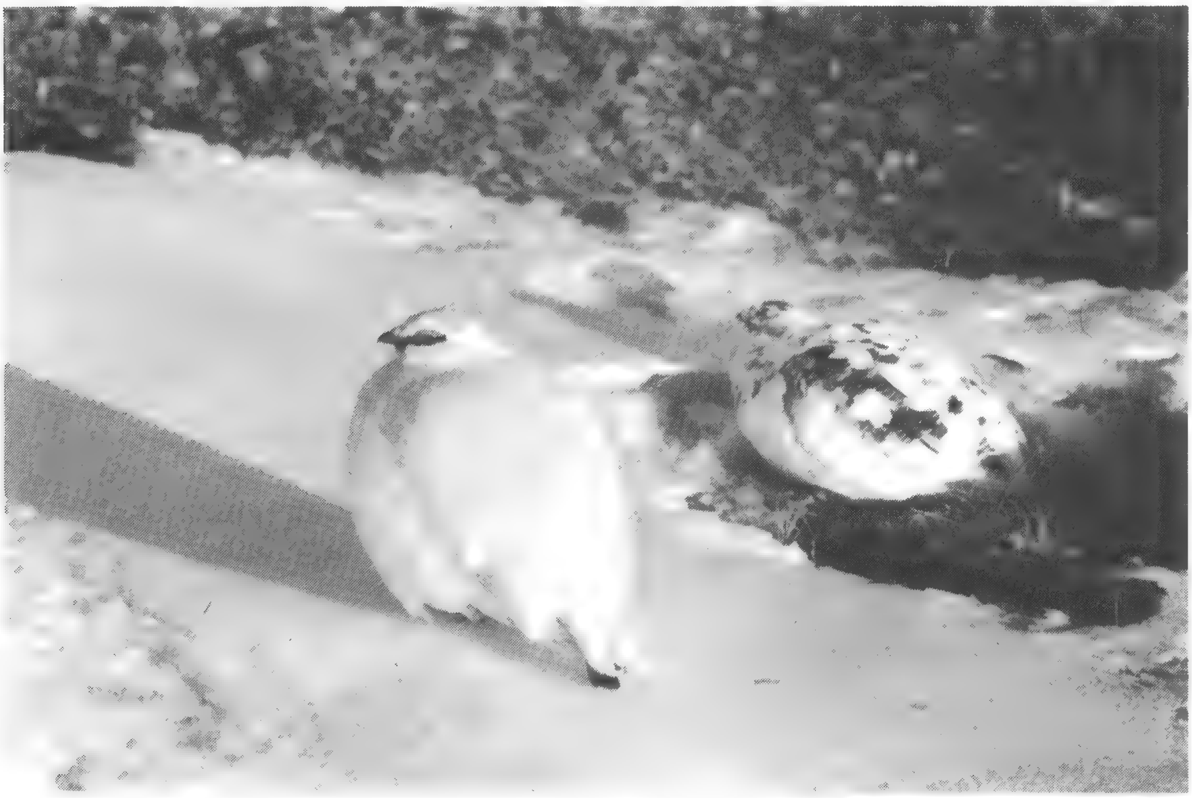


Figure 7. Male and female Rock Ptarmigan roosting at Eureka, Ellesmere Island, on 31 May 1955. Note the difference in their spring molts. The male (left) and female have selected roosting sites to match their plumage. Note also the fluffed plumage of the male and the rounded contour of the raised feathers forming air spaces for insulation. His folded combs are barely visible and the first brown feathers of summer have appeared on his crown. Photograph by David F. Parmelee.

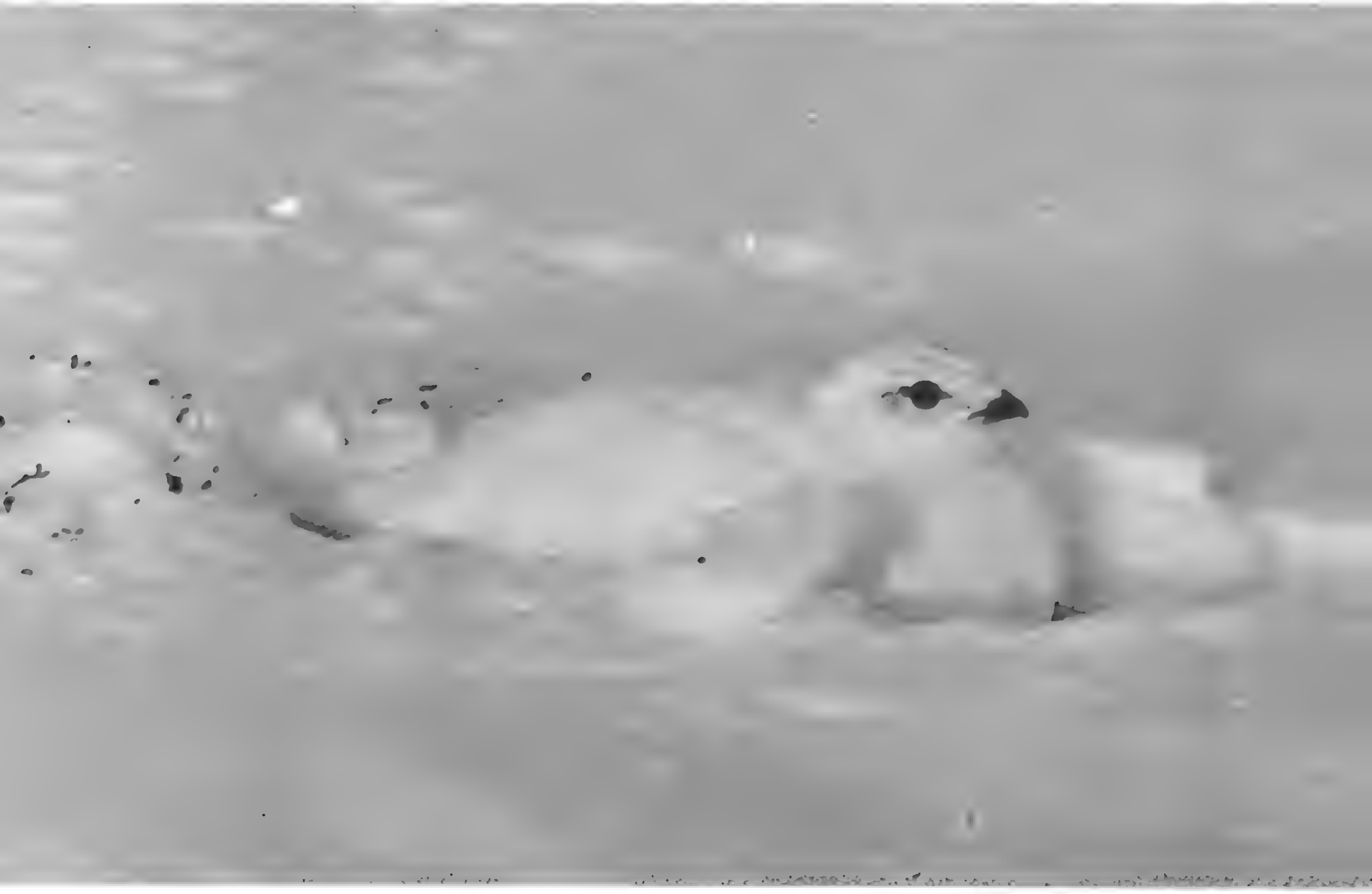
Roosting Behavior.—After feeding, when the weather is cold, Rock Ptarmigan crouch in the feeding area with fluffed plumage and heads drawn down on their shoulders, presenting an almost rounded profile (Figure 7). They often select a shallow depression between hummocks or low snow drifts where their backs are at the same level as the surrounding surface irregularities. If it is exceptionally cold or windy, they frequently excavate a depression in the snow with only their heads above the surface (Figures 8 and 9). In digging shelters they scratch vigorously like a domestic fowl and throw out puffs of snow behind them as their bodies disappear. When digging in shallow snow, they also throw up fragments of plant materials. We found, as did Sutton (1967), that Rock Ptarmigan readily roosted or sheltered in our footprints in soft, deep snow. At Bathurst Island, they also sheltered from the wind and blowing snow behind projecting rocks or in the lee of a prominence above which a slightly raised head could scan the area for approaching danger. Once a bird selected a shelter, it almost always remained facing in one direction. The accumulation of droppings at one end of the shelter indicated that the bird took its position and kept it until its crop was empty.

During this period, male Rock Ptarmigan show only very low intensity reactions toward each other even when females are present. Groups of three or four males fed and sheltered together at 14:55 and 17:35 hours on 13 May. They did not fly when approached, and were reluctant to be separated from one another. Dominance patterns appeared at this time as one male displaced another from its feeding and sheltering spot, simply by approaching directly, bowing its extended head and neck, and giving a guttural *e-r-r-r-r* note. We saw no displays involving the exposure of red combs or black rectrices. Before the males show attachment to a specific area, they seldom expose the full expanse of the spread rectrices in flight and the take-offs and landings are frequently silent.

Development of the Pair-bond

Some male Rock Ptarmigan at Bathurst Island were attached to a specific area by 10 May. Taylor (1969 field notes) approached a male which ran away with lowered head, displaying black rectrices. On 12 May he saw a pair feeding on an exposed terrace. The male positioned himself between Taylor and the female, made a soft *kruk-uk-uk-uk-uk* before flying, and the female followed him. Taylor saw no sign of combs and heard no flight-call. At this time, the male is not strongly attached to either the female or a specific area and, in most cases, will fly first. Once both attachments form, the male is reluctant to fly. He becomes vocal, raises his combs and tail, and makes himself conspicuous. Should the female fly, the male follows instantly, calling loudly. As they fly away, low over the snowy landscape, their white bodies blend into the snow-covered background and one marks their progress by their partly spread black rectrices and, sometimes, by their fleeting shadows over the snow. The female seems to determine the length of the flight since she alights first. The male immediately gives a flight-song, alights nearby, and displays his widely spread tail as he approaches her (Figures 10 and 11). Frequently, a male will perform the same display after alighting even without a female.

Figures 8 and 9. A male Rock Ptarmigan (Figure 8, *above*) looks on in watchful stance while a female (Figure 9, *below*) digs a roosting form in the snow. Note the snow and pieces of vegetation that she has kicked out behind her. His combs are erect, his plumage fluffed, and rectrices showing. Photographs by C. G. Hampson.



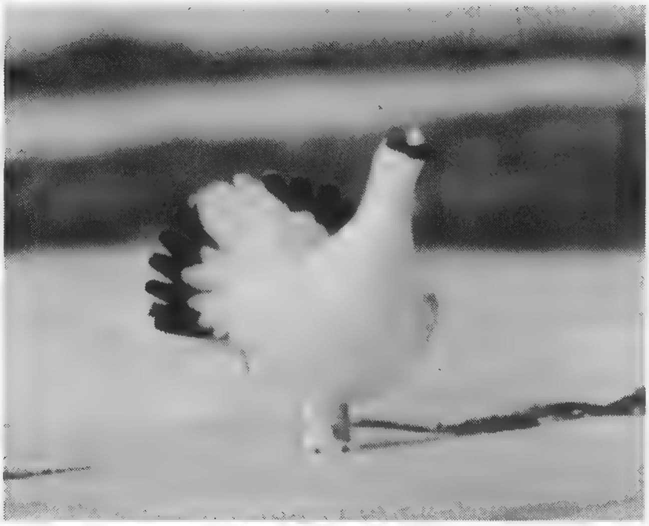


Figure 10 (*left*). A male Rock Ptarmigan landing after a Flight-song Display. He flips the fully spread tail vertically so that the black rectrices, showing for at least half their length, project like fingers. He stands with neck erect or makes a short run uttering a ratchet-like staccato call.

Figure 11 (*below*). Mounted birds, set up on known territories, often stimulated the owners to display. Here, a male circles a female mount and fans his tail revealing the black feathers. The cord, on the right, leads to a microphone covered by a blast filter.

By 13 May the development of aggressive behavior signals the dispersal of males which until now have been feeding and roosting together. The first aggressive patterns we observed were an increase in vocalizations on the ground, head bowing, and partial exposure of the combs. Dominant males displaced other males at feeding and sheltering spots as well as in roosting spots. We saw males react to the presence of another male before they appeared much interested in females. On 26 May, six males and one female roosted on an exposed terrace at 19:00 hours. Three of the seven birds had heads turned back and tucked under their scapulars with eyes and bills completely hidden. Two hours later the flock was feeding on *Dryas* and purple saxifrage along the terrace. One dominant male raised his combs and made a belching call when another male crossed his path, chasing the trespassing male a foot or so each time. None of the males showed much interest in the female; typical flock feeding behavior was prevalent; and there was no true courtship. This flock disappeared before 23:00 hours and we did not see it again. Possibly they were a migrating flock en route to the home ground (Parmelee, 1968 field notes) since birds seen a week earlier were more advanced toward courtship behavior.

We have no concrete evidence of how pair-bonding is initiated. Our field notes suggest that the male gradually establishes himself in an area with spots for feeding and prominences for sheltering and lookout. Females soon reach the area and, since it must represent optimum habitat, one or more tend to

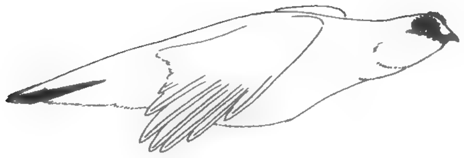


Figure 12. A Rock Ptarmigan in sailing flight. The wings bow downward and the primaries hum. Territorial males fly with combs erect and tail partly spread, revealing some of the black tail feathers.

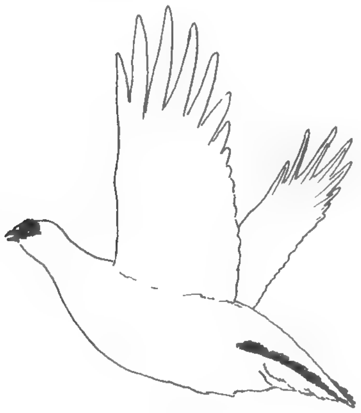


Figure 13. A male taking off in flight. His tail is widely spread and slightly keeled, again revealing the black feathers.

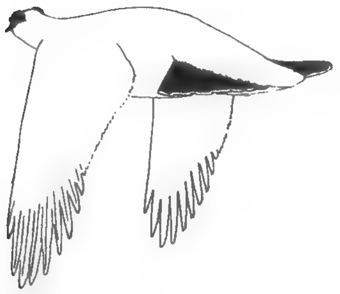


Figure 14. When taking off from his territory, the male utters a loud, ratchet-like call.

develop a strong attachment to it and become more reluctant to leave it than do the males. During this stage the male leads the female in flight.

When one female (or more) remains in the male's area and follows him in flight, his aggressive patterns become more pronounced, he vocalizes on the ground and in flight more frequently, he exposes his combs almost continuously, and spreads the black rectrices widely in flight (Figure 12). He increases his aggressive attacks on other males both on the ground and in the air, frequently flying more than a quarter of a mile to investigate another ptarmigan in the air. When the male's attention becomes so firmly fixed to both the territory and the female that he is very reluctant to leave either, the female frequently initiates a flight and the male follows her closely in the air and later on the ground. When alarmed, the female is usually the first to fly.

Territoriality.—Male Rock Ptarmigan defend large areas at Bathurst Island. In 1968, each of seven males occupied a territory of about one square mile, and each territory included several lookout prominences adjacent to moist, well-vegetated, hummocky tundra. The lookout posts are the male's activity centers from which he moves out in all directions to feed and to engage other males in aggressive encounters. The territorial boundaries are not well defined and males from adjacent territories move back and forth quite freely as long as the territorial owner is not in sight (Figures 13 and 14). Should the territorial male detect the presence of another ptarmigan, he investigates immediately. He drives away trespassing males and courts females. In our experience with high-arctic Rock Ptarmigan, polygamy occurs more often than has been recorded. We observed several males with three females periodically, and we know that one male at Bathurst Island mated with three females nesting in his territory.

During the early part of the breeding season, about 28 May, when the male has just become firmly attached to his territory, he spends much of his time in advertising display-flights, accompanied by loud vocalizations. These displays are apparently linked with the individual's aggressive inclinations and, consequently, his androgen level. The height of the Flight-song display increases along with the size and brilliance of the combs and the onset of breeding behaviors, and reaches its peak along with sexual activity.

We have banded too few adults to make definite statements about territorial fidelity. In 1968, we banded two females and color-marked one male. In 1969, we banded only one male. In 1968, the marked male vanished after 20 July. The two banded females returned in 1969 to the same hillside where they had nested the previous year, and one remained during June but we did not find her nest. This territory, occupied by one male and three females in 1968 and frequented by two males in May 1969, was optimum habitat, yet no male claimed it in 1969.

Displays of Interacting Males.—The first indication of aggression between males appears in competition for favorable feeding, roosting, or sheltering spots. The dominant male simply rushes at another bird, either male or female, and pecks it on the back. Following that encounter, the dominant bird can displace it again simply by approaching it directly or by chasing it a foot or so. Such displays at first are silent but, once on the breeding ground, vocalization and head-bowing become a common pattern. Vocalizations soon become part of displacement activity and threat patterns develop rapidly. The combs, concealed until this time, become vivid red and partly exposed during the encounters. The bird often exposes rectrices while on the ground and spreads them widely in flight. Flocking ceases under the pressure of constant threatening by males, and most males move readily into suitable habitat where they are undisturbed. The females, adopting a submissive posture, move about with heads pulled down on their shoulders and tails depressed. Frequently one male resists the attacks of the bird which seemed dominant and a contest for the area ensues.

On 28 May, one male, in making complete Flight-songs and complete ground-displays, seemed to have established himself as a territory owner, as had a second male on the other side of the hill. Each seemed to be unaware of the other until he saw him rise above the crest of the hill in a high Flight-song. Then the second male's challenge to the other resulted in vigorous aerial chases which continued intermittently until the first disappeared on 6 June.

Rock Ptarmigan are remarkably strong fliers, possibly the strongest of all grouse. Their wings are long and in flight the narrow primaries whistle audibly. The flight pattern is typically grouse-like with a short series of rapid, whistling wing-strokes, followed by a much longer period of sailing accompanied by a continuous humming of the primaries. On 2 June, two males flew through camp, announced by the sound of their wings. Their combs were

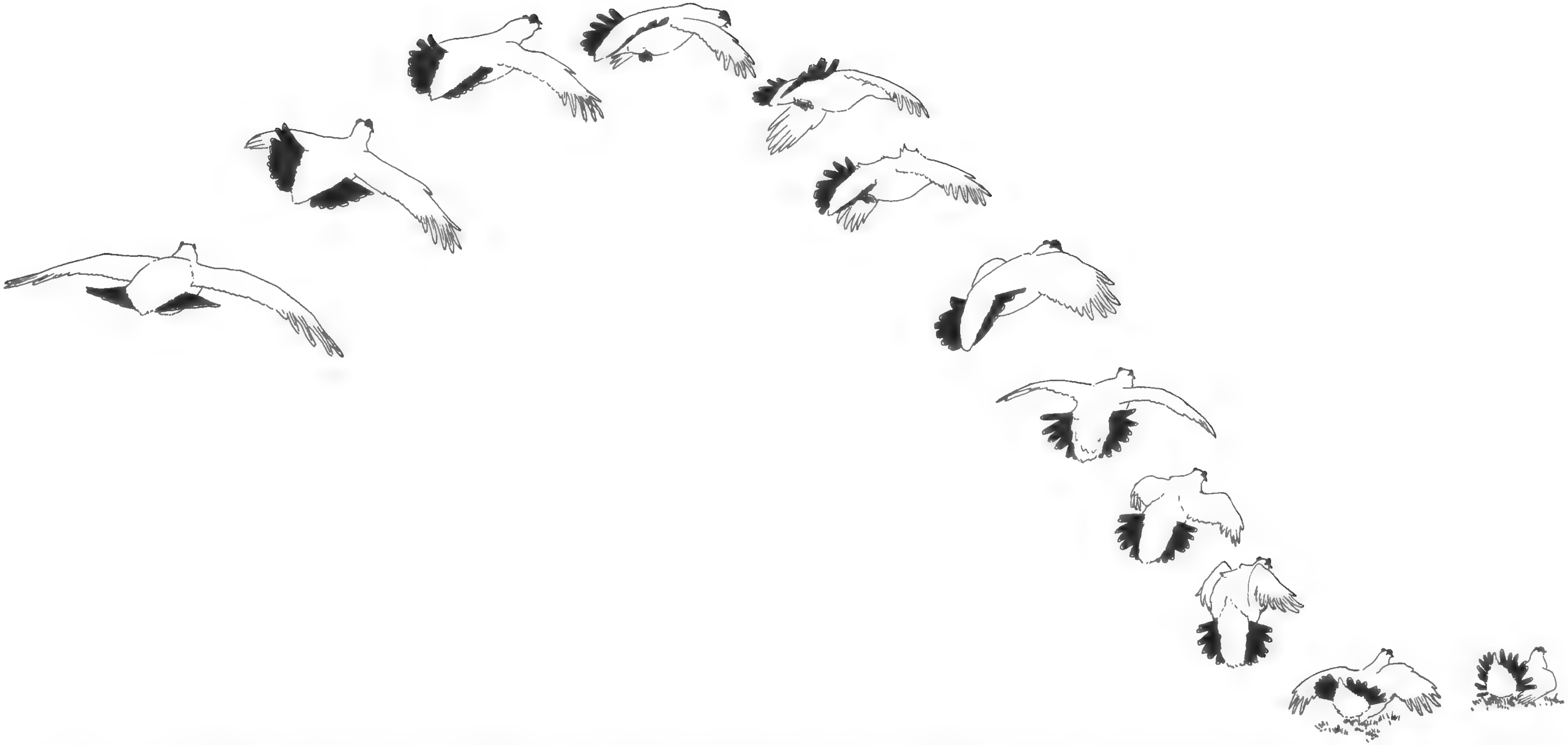


Figure 15. Drawings from a sequence of photographs of a Flight-song Display of the Rock Ptarmigan. Starting from the left: The male glides upward. Note the long wings, the widely fanned tail, and the feet held forward. Near the peak of the upward glide, he begins to sing, causing the throat to bulge. As he reaches stalling speed, the neck is bowed downward and the back of the neck bulges. The tail is deeply keeled; the lateral rectrices are almost horizontal with the trailing edge of the wings. In his parachuting descent, he curves the lateral rectrices upward and keeps the central ones down, while the turbulence raises the feathers on his back. Continuing down, he flattens as the body moves into a more vertical position. With gaining momentum, he again glides as he delivers the second sputtering part of the song. After alighting, he tips the tail up, conspicuously marking his position, and utters a vocalization, further attracting attention to himself.

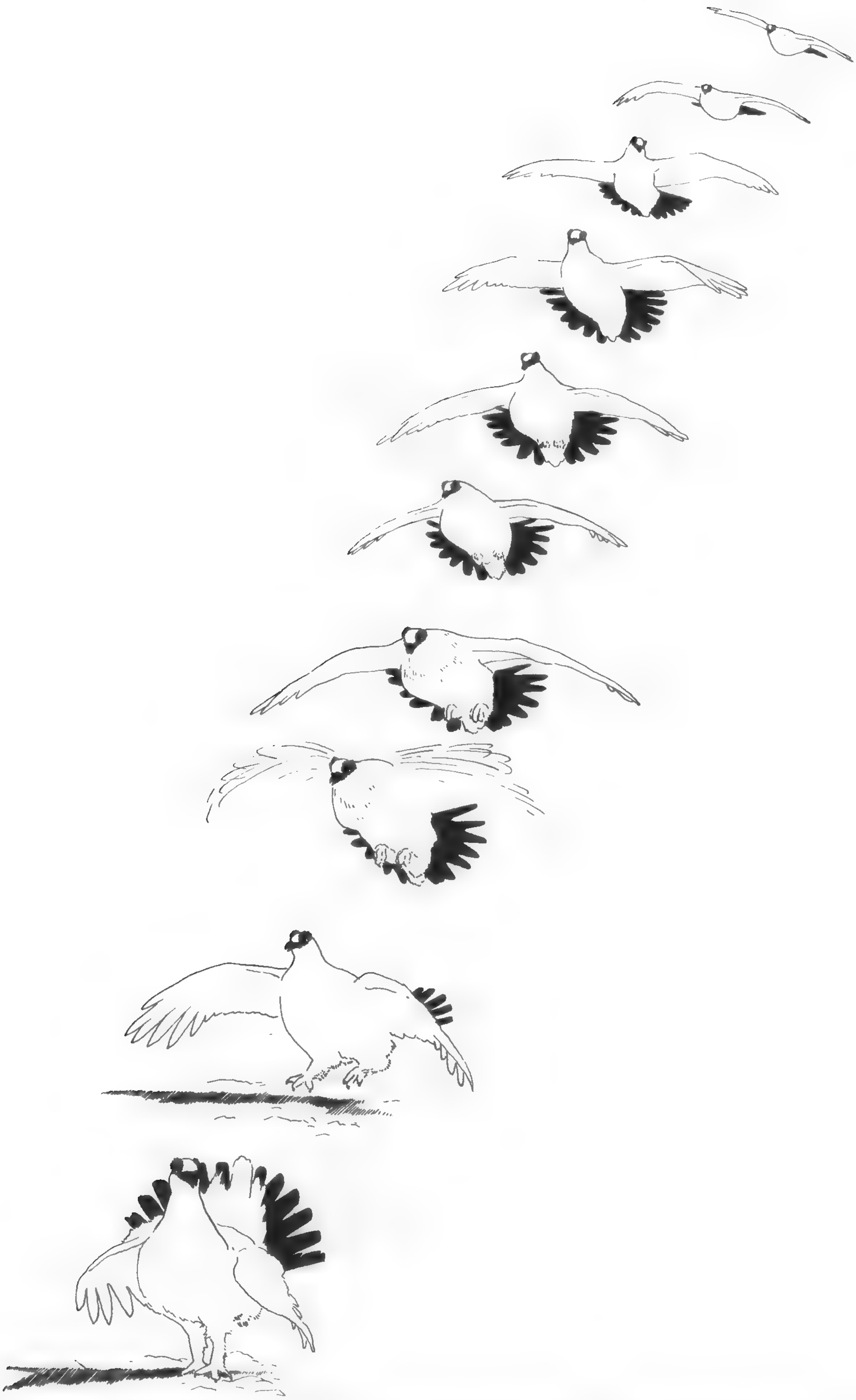


Figure 16. Drawings from a sequence of photographs showing the parachuting descent in a Flight-song Display. Compare with Figure 15 and note the ending with a ground display.

fully erect, their tails widely spread, and their bodies rocked from side to side in their vigorous flight. The exaggerated side-to-side rocking makes the widely spread black tail more conspicuous since one sees it in a variety of planes rather than as a flat surface. They continued to the crest of the hill where the chasing bird glided steeply upward in a Flight-song, then landed, displayed on the ground with croaking vocalizations, and finally flew back toward his own territory and repeated his Flight-song. The other bird continued on his downhill glide and gave a Flight-song and ground-display when he reached his territory.

Aerial chases take place anytime, day or night, but most display activity occurs between 21:00 and 03:00. Strong winds with or without blowing snow inhibit displays (Watson, 1956) while low wind velocity and bright sun elicit greatest display activity. After a period of bad weather the frequency of displays rapidly increases. The birds we studied responded to playback of recorded Flight-songs with displays, suggesting that the display sounds of other males may be necessary to stimulate the activity. Frequency of Flight-songs is higher in a large population than when the population is smaller with individuals more widely spaced.

Watson (1956) observed patterns of behavior which did not occur at Bathurst Island. This is apparently due to the hyperstimulation of a large breeding population. He also refers to a "sexual chase" which the male initiates by forcing the female to fly, and once in the air the pair may be joined by one or more unmated males. During these flights the male may dive at the female and attempt to mount her in midair, or he may spar with another male. We did not record a single sexual chase during two seasons at Bathurst. In fact, the attempt to mount in midair is contrary to the behavior patterns leading to copulation in the Bathurst Island birds. The copulation attempts we observed were so leisurely and extended so unhurriedly over such a period of time that at first we thought them atypical. We observed two, occasionally three, males in aerial chases; none involved females.

Flight-song Display.—This is the most spectacular of the displays of the Rock Ptarmigan (Figure 15). The visual aspects, coupled with loud, far-carrying croaking or belching vocalizations, serve to effectively advertise and mark the position and territory of the male. It is an elaborate development of the drumming and flutter-flights seen in other Tetraonidae and, like them, it is a functional visual signal involving parts of the body which are highly contrasting in color.

The Flight-song relates directly to the male's aggressive feelings and the strength of his attachment to his territory. Linked with this behavior is the enlargement and display of the combs as well as the increased intensity of their color. Watson (1956) believed that peak singing probably coincides with the period of most rapid increase in the size of the comb and that this secondary sexual character is receptive only to androgens. Our observations seem to support his opinion in that Flight-songs do not occur until the male begins to show territorial attachment and to display the vivid red combs. The onset of both of these displays is gradual, and the Flight-songs increase in height from less than four feet, when males are establishing territorial claim during the last few days of May, to an estimated 250 feet when a highly aggressive male is on his territory in late June.

The Flight-song may be spontaneous, or it may be initiated by almost any disturbance in the male's territory. Watson (1956) reported that males displayed in response to gun shots and human intrusion. We also observed Flight-songs in response to the entrance of another ptarmigan in an established territory and to the approach of caribou, muskox, arctic wolf, and arctic fox. When the territorial male flies, he takes off with a loud, belching call, and sings as he descends and on landing, and continues on the ground with vocalizations and another display.

The Flight-song follows a stereotyped pattern, and is likely to be incomplete in the beginning and at the end of the territorial behavior. The complete display begins when the male leaves his territory. He springs into the air on a noisy take-off with whirring wings and a loud belching call. He fans the tail widely as he flies away, usually at a low elevation, following the contour of the land. The flight is swift, with rapid, whistling wing-strokes followed by a brief period of sailing. These two patterns alternate and may carry the bird a few hundred yards or a quarter of a mile or more before he delivers the song. The male almost always gives Flight-songs as he clears the crest of a hill, at the edge of a bluff or an escarpment, and as he soars upward into the wind at the end of the flight. With wings bowed downward to their fullest extent, the primaries widely spread, and the alula quills extended in scaling flight, the male inclines his body and, with head thrown up and back, soars steeply upward. At the same time he fans the tail to its greatest extent, separating the three outer rectrices for most of their length. The central rectrices and the white upper tail coverts are depressed to form a keel-like extension of the body. The three lateral rectrices are now almost horizontal, forming a planing surface continuous with the trailing edge of the secondaries. He holds this position on the soaring, upward flight until he reaches stalling speed. In this phase he swells the neck and begins the first, staccato, far-carrying belching notes of the song. Momentarily, the bird hangs in midair, and, as the song begins, bends the head and fully extended and inflated neck downward. This movement causes the neck to bulge dorsally and the bird to descend. The second portion of the belching notes begins and lasts about one and one-half times as long as the first series. The air pressure increases against the four outer rectrices and curves them upward at their tips. While their plane surface remains flat, or horizontal, the remainder of the tail is depressed to form a more deeply keeled profile which gives a parachuting effect as the bird floats downward. The slotting of the primaries and outer rectrices provides sufficient lift to raise the dorsal plumage on the wings and back. From this point the descent is rapid, and the second longer vocalization is heard as the bird flutters to the ground. Just before alighting he swings the body into a more upright position, and holds the widely fanned tail vertically downward. Even from a distance the sharply contrasting black and white is remarkably conspicuous. On landing, the tail, still fully spread, is flipped up vertically, a movement marking the bird's position on the ground (Figure 16).

A ground-display which has specific vocalizations associated with it follows the Flight-song. When he flips the tail up vertically, he does not fold the wings completely, and often several of the longer primaries catch briefly between the first or second rectrices on each side (Figure 17). This perhaps assists in holding the tail so widely spread that most of the rectrices are separated at their tips for half their length. The tail fan becomes a striking array of black, finger-like projections. Usually the male stands with neck erect or makes a short run in this position while uttering a ratchet-like, staccato call which he may repeat two to five times. This ground-display is discontinued when the female begins incubating.

Following this brief pause the male bends his head slightly downward so that the bill is below the horizontal. His neck, almost fully extended, becomes slim; the breast becomes much wider because the long contour feathers on the sides spread laterally, kept in that position by the wings which he holds loosely, away from the body. He lowers the brachium or upper arm so that the forward-spread alula almost brushes the ground and the partly spread primaries drag along half their length, making their blackish shafts conspicuous. He spreads the tail to its fullest in a flat fan and holds it at about 45 degrees. Then, leaning forward, he begins a short stepping run for three to 20 feet. As he goes, with his head and the extended neck bowed downward so that the tip of his bill almost touches the ground, he resembles a mechanical toy (Figures 18 and 19). In soft snow the primaries make wobbly striations, and on crusted snow they make an audible scraping sound. Throughout the Flight-song and the ground display the vivid red combs are prominently erect. The slow, bowing movement presents them conspicuously against both black and white areas of the plumage. If a female is present, he runs in an arc toward her. He tilts the tail toward her, presenting always the maximum area

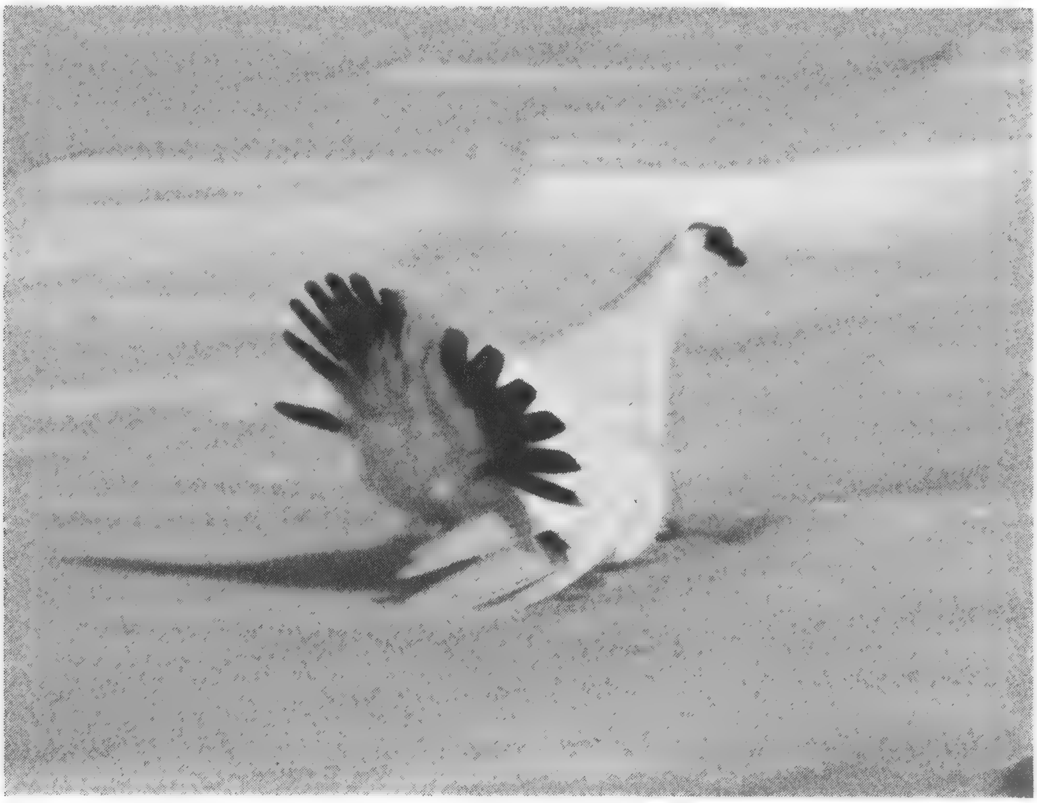


Figure 17. A courting male Rock Ptarmigan approaching a female after a Flight-song. With scarlet combs raised and spread tail tilted in her direction, he runs in an arc toward her. Note that the primaries catch and pull down the lateral rectrices, causing the others to spread even farther apart.

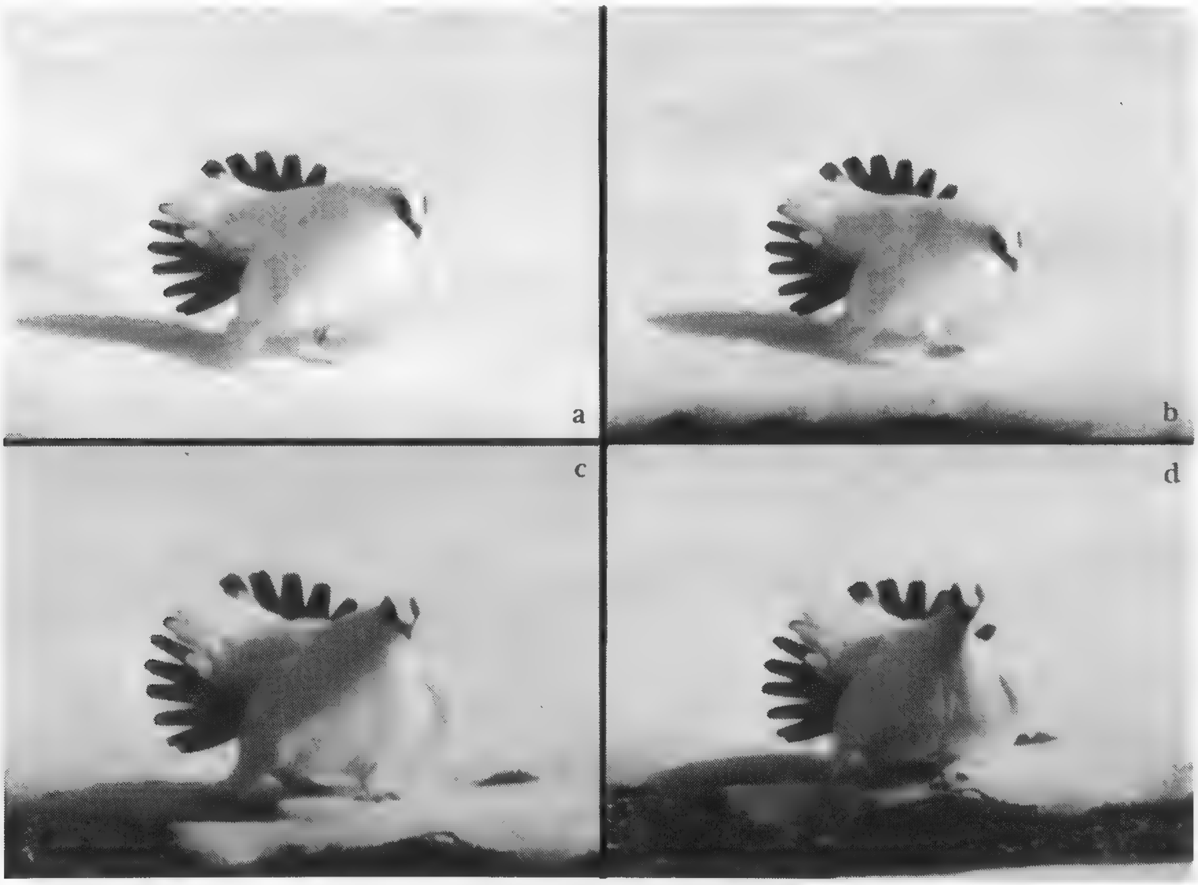


Figure 18. Four sequential views from left to right (beginning with upper left) of a male Rock Ptarmigan giving a courtship display after a Flight-song. The interval between each picture is one-third of a second.

of black, and extends the wing free from the overlapping breast feathers and away from the female. During the single bowing movement he holds the head and neck oblique to the midline of the body and toward the female, thus making both scarlet combs visible to her at once. He omits this display shortly after the female becomes established on the territory and copulation has occurred. Although he often directs this display toward a female, it is a common component of the territorial display and strongly marks territorial occupancy. I have never seen a trespassing male give it in another territory. Trespassing males always take a very watchful stance even though they may have made a Flight-song when alighting in the other's territory, a behavior that always elicits vocal and visual threats from the owner in early territorial occupancy and an instant attack later in the season (Figure 20).

Aggressive Behavior of Males.—Males with adjacent territories spend much effort in threat and advertising displays. Many encounters are simple ritualized fighting with vigorous chases on the ground and erratic pursuits in the air. Some males never seem to establish a clearly delineated boundary between their territories. Rather they develop areas of "no man's land" where they meet with threatening vocalizations and violent battles, frequently drawing blood and tearing out feathers (Figures 21, 22, and 23).

The territorial male's aggressiveness increases steeply as the female becomes more receptive toward him and when copulation is imminent. During this period we observed violent fights between rival males, often from close range since both males are almost completely oblivious of anything except their opponent. I saw such a fight in detail on 16 June as I was watching

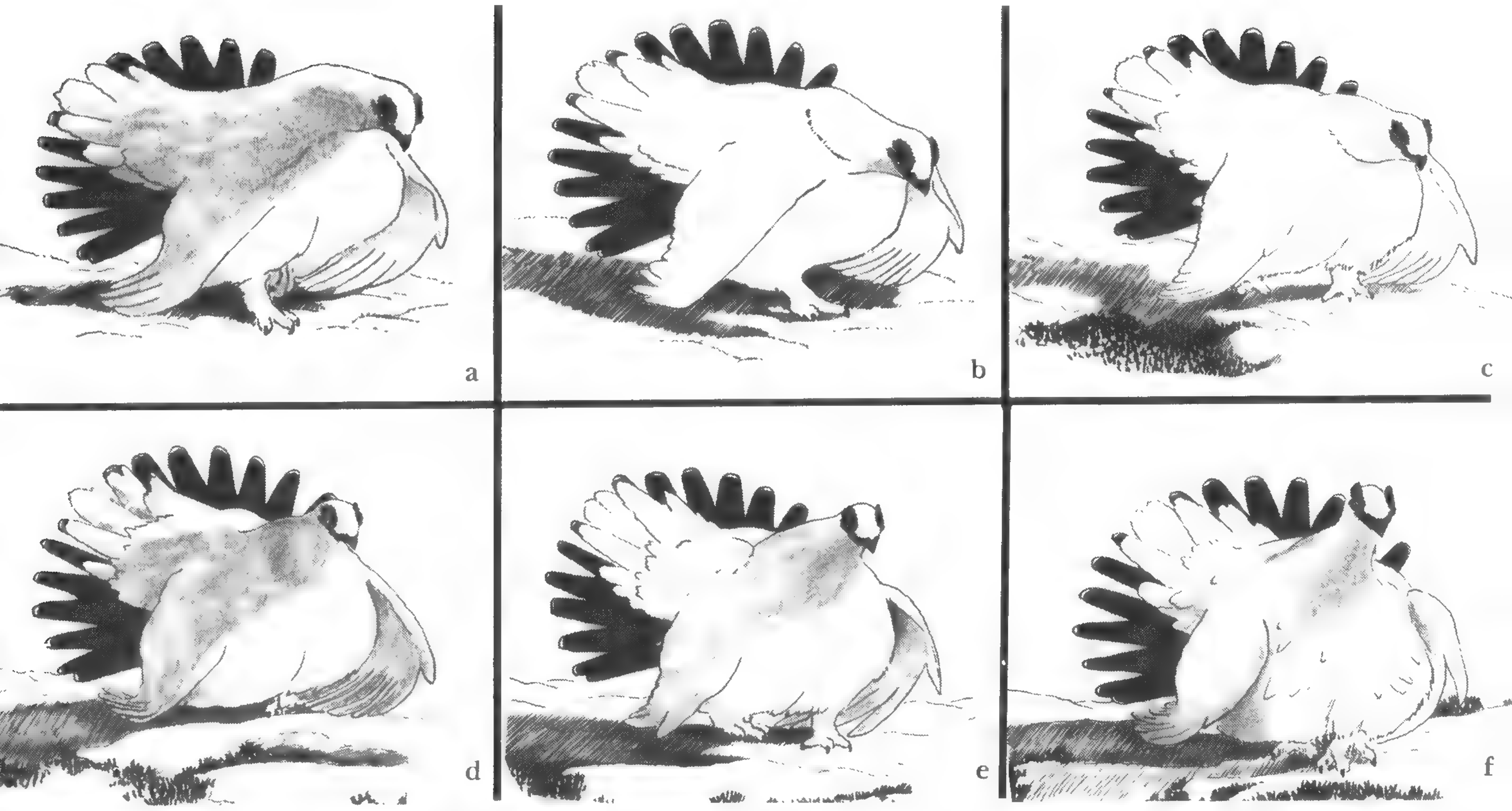


Figure 19. Drawings of the complete ground display beginning at upper left, as in Figure 18. This display lasted two seconds.

a pair that had copulated two hours previously. The male had begun a series of Flight-songs to and fro at three to five minute intervals from the ridge, where the female was feeding, to a marsh about 1,500 yards down slope. I wrote the following in my field notes.

18:32 hours. Male 1 returned, made a Flight-song, landed 40 feet from female, and began to walk toward her, showing a black wedge of his tail. Suddenly, he became very alert and flew off without calling; he landed about 20 feet away and ran to meet Male 2 which had arrived silently from the other side of the hill. The female flattened herself in a small depression among the low hummocks and remained motionless. Both males began running parallel to each other about five feet apart. They ran about 10 feet with tails partly spread and horizontal (Figure 24). The rectrices toward each bird were tipped downward to expose a triangle of black. The combs of both birds were vivid red and extended above the crown line. Each made loud ratchet-like vocalizations and both birds waved their extended necks up and down in a snake-like movement at each pause. They continued running with the bills tipped slightly upward, the wings were held slightly away from the body, and the primaries spread to expose the black shafts.

Suddenly Male 1 ran at Male 2 and stopped about 18 inches in front of him. Both birds made loud, drawn out ratchet-like crowings and simultaneously arched and lowered their extended necks until their wide-open bills pointed vertically down. This movement emphasized an oblique presentation of the combs, and the neck bulged prominently at the back during the call. Male 1 darted at Male 2 which jumped over him with two or three wing-strokes. Male 1 then sleeked his plumage and adopted a stance with his tail horizontal and very little black showing. His extended neck was also horizontal and lowered so that his chin almost touched the ground. His long crown feathers were fully erect exposing their gray bases, and the black facial markings became enlarged. The combs were completely hidden. The raised plumage on the head emphasized the gray bases of the crown feathers and, with the black facial markings also fluffed out, the contrast was striking and made the bird's head appear much enlarged. All of his movements were low to the ground, and he ran around and around Male 2 as if he were trying to crawl under him.

Male 2 kept moving away in a sidling fashion with his tail spread three-quarters and tipped sideways, his head and neck lowered and extended, but not as low as Male 1's. In this position, with his combs still erect, he ran off about 10 feet, stood, made another ratcheting call, and bowed his neck down. Male 1 ran at him and instantly seized him by the neck feathers; Male 2 grabbed him by the upper breast plumage. Both birds jumped, flailed with their wings and tumbled over

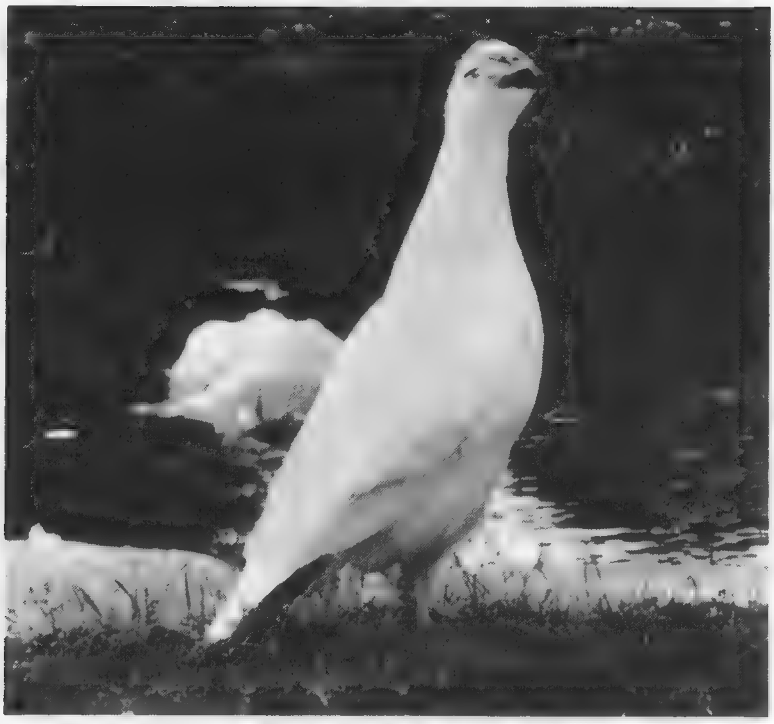
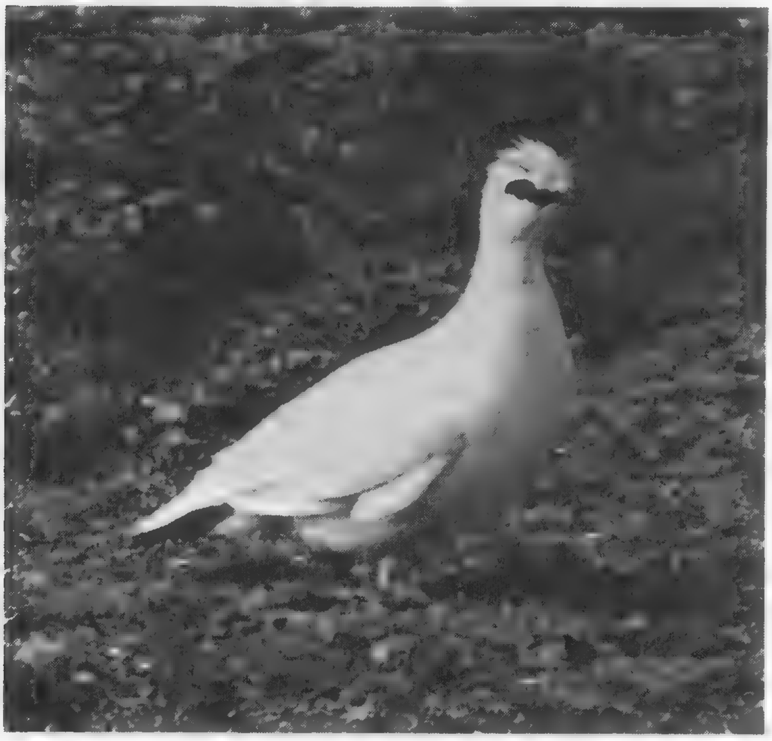


Figure 20 (*above*). A territorial male Rock Ptarmigan watching the return of a rival male as he alights nearby to continue the skirmish. Note the raised feathers on the crown and the sleeked plumage. Photograph by David R. Gray.

Figure 21 (*below*). A territorial male watches a departing male. His crest feathers are raised, showing their gray bases. This is a high-intensity reaction to a male trespassing on his territory. Photograph by David R. Gray.



and over down the hillside like a ball of rags. Each bird struggled to gain his balance by pressing his widely spread wings against the ground. After about one minute Male 2 escaped and flew off with Male 1 in hot pursuit, leaving puffs of white feathers blowing around on the battle ground. In about one minute Male 1 returned, soaring in a Flight-song to about 80 feet and landed within 30 feet of the female, still crouching in the same place. He made several croaks, tipped up his tail, lowered his head and ran up to within eight feet of her, sat down on a snow patch and went to sleep. The female, standing very low and humped, crept out of her hollow and began to feed.

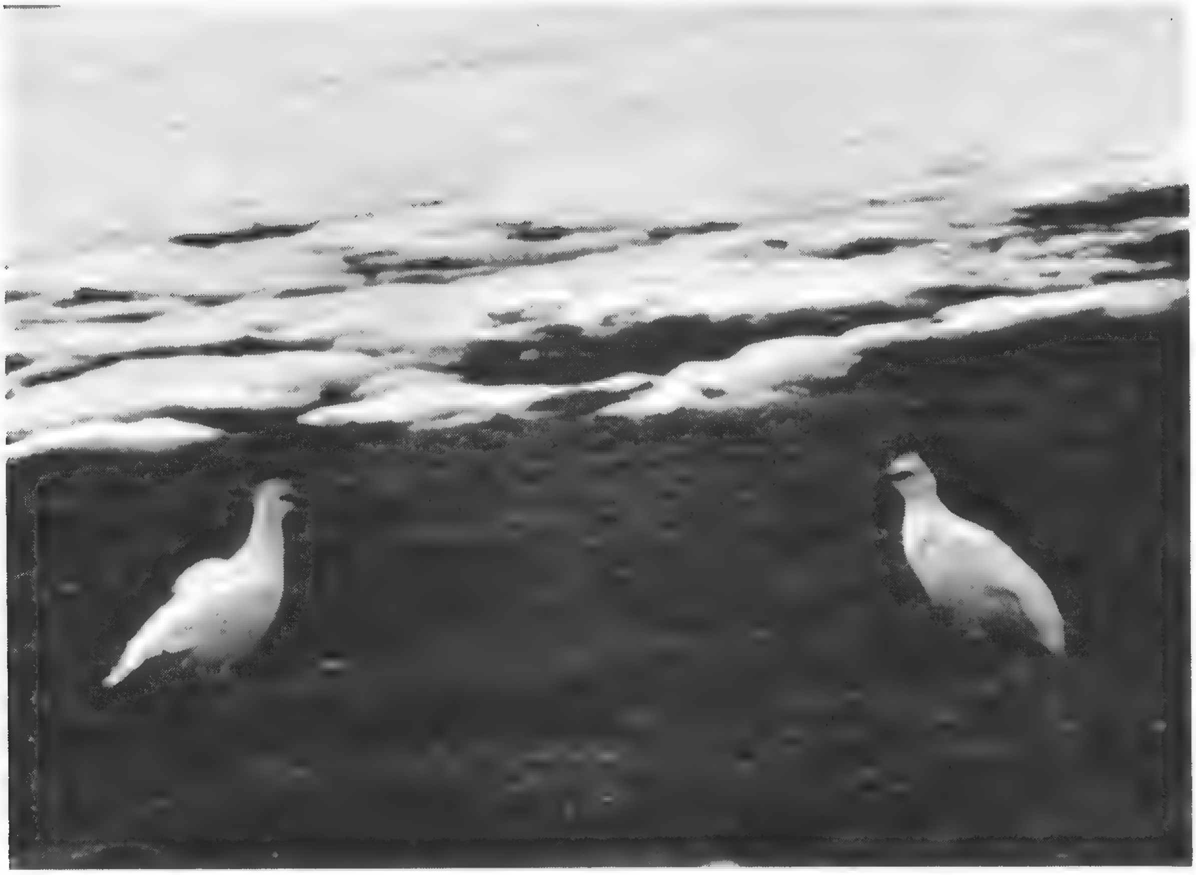


Figure 22 (*above*). Two males confronting one another on a plot of moist hummocky tundra. This was one of the two areas we knew of where these males met for ritual and actual fighting. Photograph by David R. Gray.

Figure 23 (*below*). A territorial male (left) flying at his rival and the rival about to take off in a hurry. Note the expanse of the wing and the bulging throat of the escaping male. Males move into the well-vegetated, hummocky tundra to molt after deserting their territories and mates. The lower part of a muskox skull lies almost buried in the mossy sedge hummock at the extreme left. Photograph by David R. Gray.

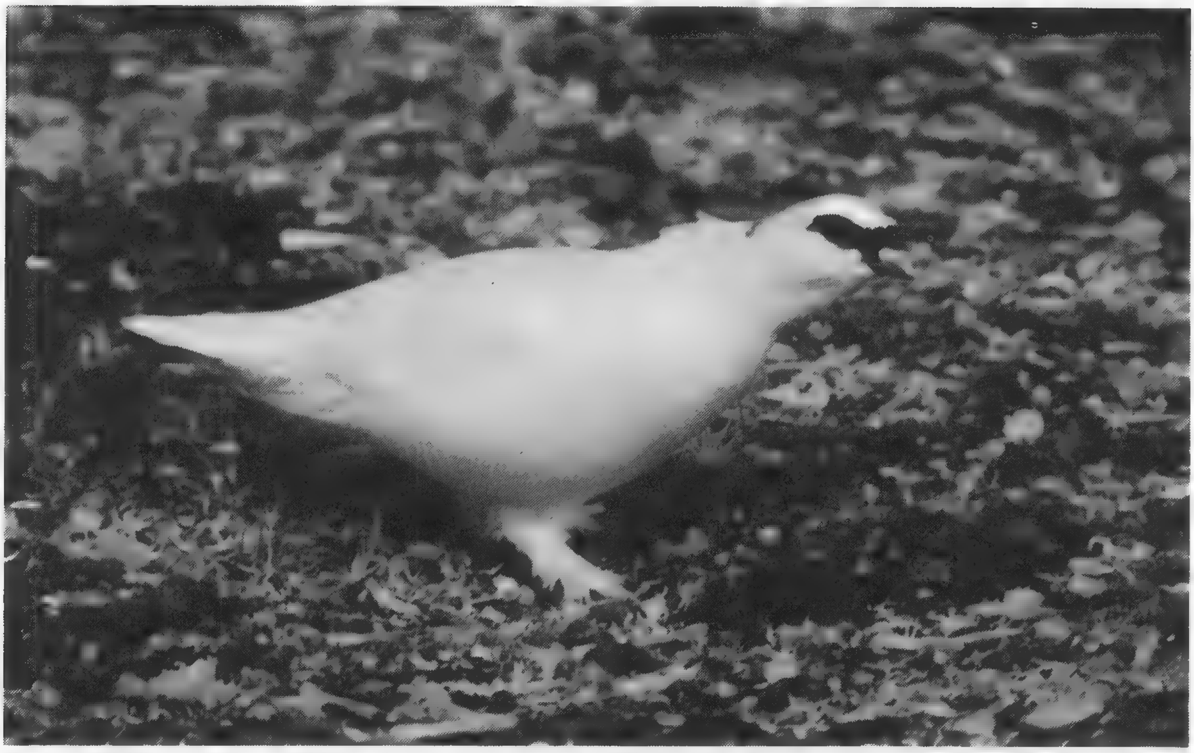


Figure 24. A male Rock Ptarmigan assuming a horizontal, threatening posture and giving a long, loud, ratchet-like challenge. His combs are partly concealed, his plumage sleeked, and his neck inflated. Photograph by Pierre Lamothe.

On 15 June 1968, I saw the following variation of the above.

A female, whose nest we had found at 12:28 and which had laid her second egg at about 14:49, was feeding with her mate at 18:39 on a grassy hummock near a small pond, 300 yards from her nest. At 18:40 the male flew off silently and the female crouched in a depression. Male 1 had not gone 200 yards before a second male flew in, sang, and alighted without a ground-display on a hummock 80 feet from the crouching female. Male 1 heard the song, made an abrupt upward arcing turn of about 180 degrees, singing as he turned and then singing again as he landed on a hummock between the trespassing male and the female, still huddled in the same spot. On landing he performed elaborately, tipping his widely spread tail toward Male 2 and dragging his spread primaries along the ground. He then assumed a more threatening horizontal position within two feet of Male 2, with sleeked plumage, black rectrices almost completely concealed, and combs fully erect and bright red. Male 2 instantly lowered himself on his belly and crept like a female into a shallow depression about three feet away, crouching with his head low and his face partly hidden among the hummocks.

Male 1 then stood very erect, began bowing with his tail partly spread and tipped toward the other male, and approached him obliquely. Male 2 crawled out of his hollow, crept into another two feet away, squatted, and began slight head jerking and squirming movements like those of a Spruce Grouse, *Canachites canadensis* (Lumsden, 1961; MacDonald, 1968). Male 1 approached in a very erect, "looking down" stance, seen in courtship and copulation, and walked very slowly to within two or three inches of the squatting male, which had completely concealed his combs. As Male 1 approached, he seemed about to attempt copulation when Male 2 moved and, still crouching, crept a few feet away to another spot where there was no sheltering depression. Male 1, quickly adopting a horizontal and threatening attitude, seemed ready to attack. Male 2 pulled his head down on his shoulders, depressed his tail in a typical female-like submissive attitude, and crept into another depression.

At this Male 1 again ceased threatening and assumed the "looking down" attitude of precopulation. Male 2 showed no sign of combs or rectrices; Male 1's combs were still large and red. Male 2 suddenly flew up and Male 1, crowing as he took off, followed closely. After a chase, five feet above the ground, for about one quarter of a mile, Male 2 landed with tail only slightly spread. Male 1 rose in a towering Flight-song 80 to 100 feet directly over him and then landed beside him with the typical ground-display followed by an aggressive approach. Male 2 again crouched in a depression and successfully blocked the attack.

Male 1 returned to the still crouching female and performed a Flight-song up to 40 feet, followed by spread tail display and dragging wings. The female completely ignored him and both began feeding.

Actual fighting seems to occur more frequently in high arctic populations of Rock Ptarmigan than among Spruce Grouse or Blue Grouse (*Dendragapus obscurus*). In most fights one or both birds lose feathers, and infrequently a piece of the comb is torn away. They use bills and wings as weapons and tend to seize and hold with the bill while flailing with the wings. They aim blows of the bill at the opponent's face, but often miss their mark, striking instead the upper neck and breast. The sides and back of the neck of aggressive males show obvious gaps of missing feathers which, when replaced with brown summer plumage, appear as spots against the surrounding white feathers. Although the fights of Rock Ptarmigan are violent – in a single encounter dozens of feathers may be pulled out of the front part of the body, and a fleeing combatant may have back, rump, tail coverts, and rectrices pulled out– I have never seen any serious damage. The flailing of the wings, though impressive, is mainly ineffectual since the opponents are holding each other so closely that they miss the full force of the blow and the spread wings of one bird act as a foil against the blows of the other.

The aggressive behavior most frequently observed between males is the erratic aerial chase during the early stages of territorial claim. Males on adjacent territories fight in midair if one can overtake the other. These fights resemble those on the ground in that feathers fall while the birds circle around buffeting each other with their wings as they flutter down.

Courtship Behavior

Pair-bonds begin to appear in late May or early June when flock behavior gives way to widening of individual distance by the males. The behavior of an aggressive male driving other males from the area brings about an obvious change in the female. She gradually abandons the independent attitude, exhibited while with the flock, and becomes dependent upon the watchful male. With head and tail kept low, she appears more rounded and the male follows her continuously with his plumage fluffed out and his bright scarlet combs fully erected (Figure 25). While feeding and walking, the female seldom raises her head above the level of her back unless alerted by the male's approach or his alarm call. During the early stages of pair-bonding before the female is strongly attached to any area, she will fly away readily if alarmed. The male, making a continuous alarm note, remains on the ground until the female flies and then instantly follows her. The female determines the direction of flight and the distance. When she alights, the male soars upward in a Flight-song and finally alights nearby.

The female, by her extended occupancy of a specific area, determines the center of activity in the territory. As she becomes more and more attached to specific feeding and sheltering areas, the male tends to select prominences nearby for lookout posts. In addition to these, he has others more prominent on the tops of nearby ridges which he visits regularly. Encounters with other males most often occur on these patrol flights. When the female begins to incubate, the male frequents these distant lookout posts even more and abandons most of those used while the female was with him.

The female's submissive attitude stimulates the male to become more attentive and to gradually move closer to her during their daily routine and while roosting. He adopts a very upright stance, his body plumage puffed out and his tail partly spread so that the black rectrices are prominent. The long plumage on his rump hangs loosely on each side of his tail. When moving about, he holds his body horizontally, raises his head and tail so that one is at about the same elevation as the other. In this position his combs are always conspicuous and the lateral rectrices contrast with the white plumage.

While the male is near the female, he gives continuous, and monotonous, ticking notes in a staccato sequence of two or three (Figure 26). This "contact" or "assurance" song, audible to humans at 20 to 30 feet, quickly changes in alarm to a ratchet-like sound resembling the line being pulled off a fishing reel. This alarm call, given by the male in an upright position (Figure 27), causes the female to flatten herself or to crawl into the nearest depression and crouch. The male, because of his watchfulness, often continues to feed after the female has finished and is sheltering in the lee of some small surface irregularity.

When the female responds to the male's alarm notes, he then makes short display-flights or engages in aerial chases with other males. He frequently calls alarm before taking off, and the female crouches until he returns one or two minutes later.

On 2 June a male returned to his territory, performed a Flight-song, and landed 20 feet from the crouching female. He then began a short run toward the female with his neck extended and his tail widely spread and tipped prominently toward her. He spread his primaries and extended the wing away from the female with the primaries touching the ground. After about six feet he changed to a walk with his wings in a normal position and his tail partly spread. The female, showing alarm reactions, stood up with her crest raised. The male stopped and, with combs raised and body rather upright, bobbed his head – a shallow nodding movement with the head moving downward in an arc. As his head moved down, he raised his tail so that head and tail were approximately in the same plane with that of the neck and back. He interspersed head bobbing with some pecking at the ground. This head bobbing differed from the same behavior in Spruce Grouse in that the tail was not raised and head movements were not as fast (MacDonald, 1968). It may be more closely related to, and is probably derived from, actual feeding behavior.

As the male moved toward the female, he began head-bobbing with a low grating note. Standing upright in front of the female as if alarmed, he partly spread his tail and tipped it toward her. The wings were in a neutral position. His combs extended above his crown, and the black facial mask was enlarged apparently by raising the feathers. With head upright, the male pointed his opened bill slightly upward and began to turn his head from side to side through a very narrow arc, seeming to expose the brilliantly contrasting black, white, and vivid red markings on the head to their greatest advantage. I, only 60 feet away, heard no sound; probably the strong wind may have deadened it. The female quickly became agitated and flew with the male following.

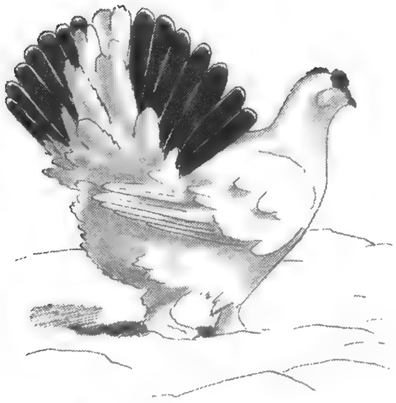


Figure 25. The male displaying the black tail feathers. He may, in the early stages of courtship, display his black feathers by holding them vertical when approaching a female.

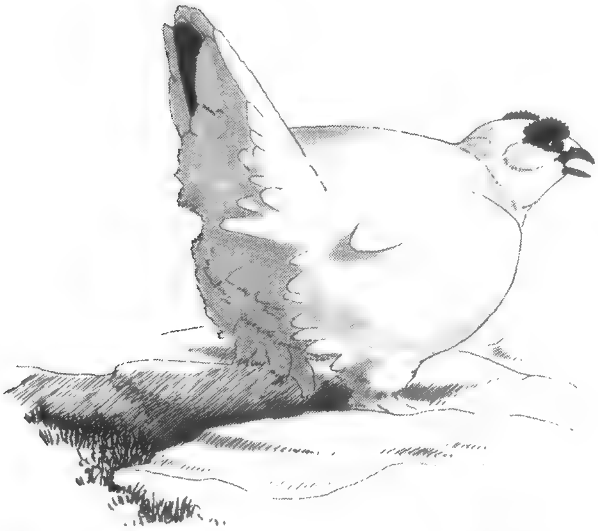


Figure 26. The male during an early stage of courtship. He follows the female with head lowered and tail raised, uttering a continuous ticking "assurance" note with the bill closed, or a "cautionary" or mild threat note with the bill open. Note how the long tail coverts extend around the black feathers of the tail.

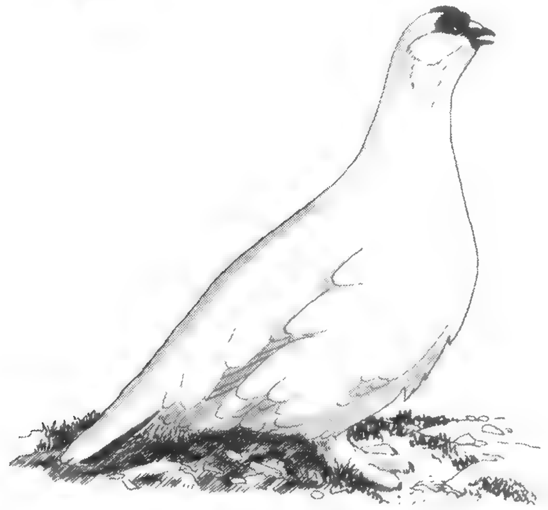


Figure 27. The male Rock Ptarmigan in alert posture. With head high and combs raised, he gives the alarm call.

These behavior patterns continued for the next ten days, with the male continuously moving closer to the female and she becoming less alarmed by his approach. By 13 June the female was three-quarters brown with the greatest concentration of dark plumage on the scapulars, back, rump, and upper tail coverts. Her head, completely mottled, looked like a lump of dirty snow, an effect enhanced by the fact that she spent most of her time near small snow patches or at the edge of the bare ground (Figure 28). The still white male spent most of his time on the white snow.

While the pair was on the ground, the male followed the female at about 18–24 inches and courted her almost continuously. With his head held low and his partly fanned tail tipped toward her, he made brief Circling displays

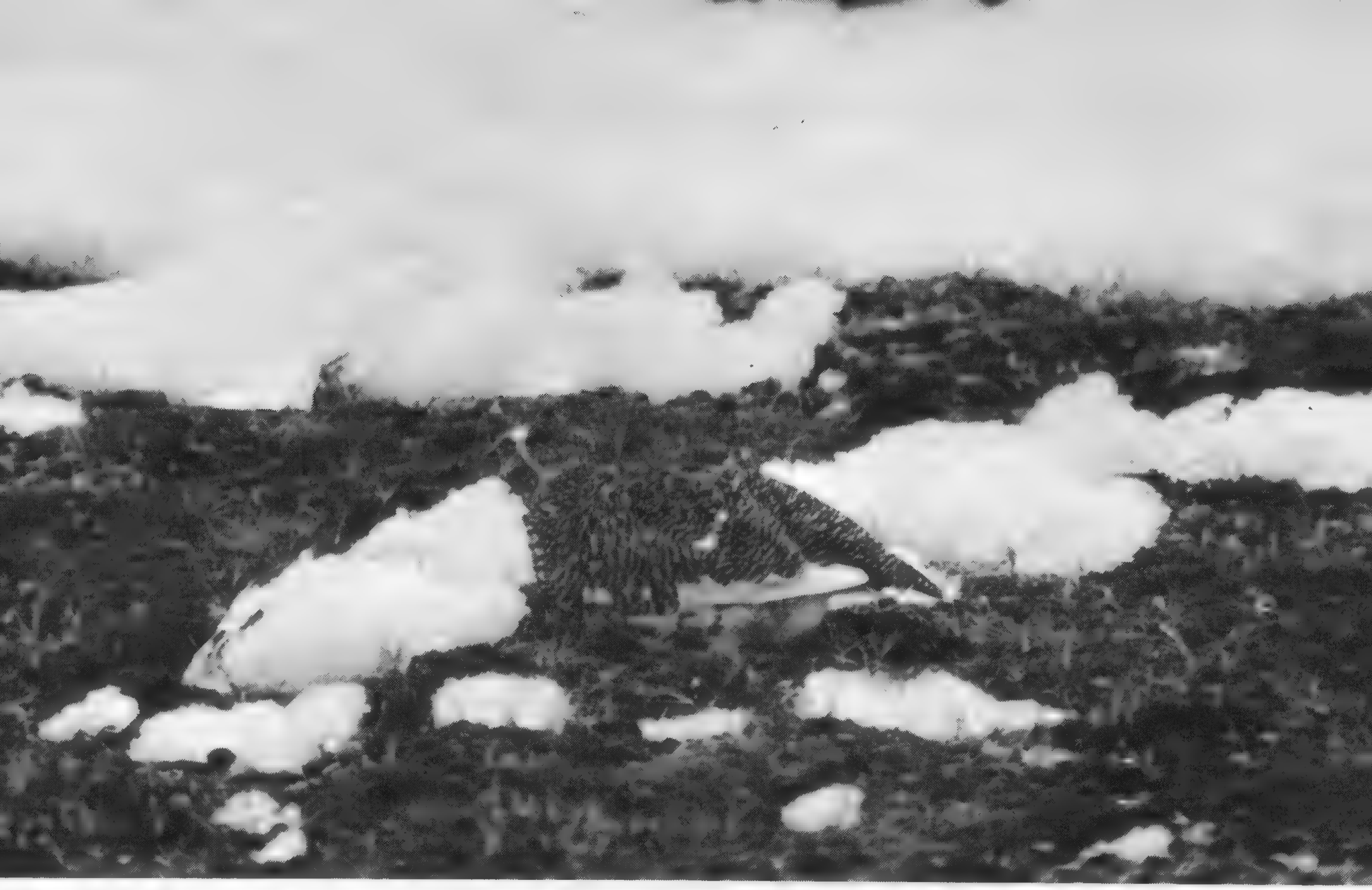


Figure 28. A female Rock Ptarmigan feeding on a bare spot at the edge of a snow mass. Females often search for food around the edge of the melting snow, in places where the background blends best with their incomplete summer plumage. Photograph by Pierre Lamothe.

with primaries extended and their tips dragging. If he approached too closely, the female crouched and crept away in a humped position with her head pulled down on her shoulders and her tail depressed and dragging the ground. Her black rectrices were always completely hidden. If he continued to approach, she turned abruptly away. Still displaying, he moved in half circles around her trying to halt her, and to direct her toward the nearest depression. Frequently he ran ahead, holding his neck so low it almost touched the ground, and crouched in the depression himself apparently trying to induce the female to crouch in it for copulation. If the female approached any small hollow, the male, displaying his tail and combs, sidled toward her and crouched at the edge of it.

When the female becomes attached to the area, the male does not hesitate to leave her. If he flies in alarm, she may follow or she may crouch in a depression. When the male readily leaves the female in his territory, I consider the pair-bond secure. The female at this time appears heavy bodied, no doubt due to the rapidly enlarging ovary, and her take-off is somewhat labored with deeper wing-strokes and more flapping between the periods of sailing. This is probably why the female prefers to crouch among the hummocks rather than fly. If she crouches, the male gives an alarm call and flies off as if he were alone, giving his Flight-song as he alights, and again as he returns to the female.

Gray noted unsuccessful copulations on 13 June, and again on 14 June. Apparently, no postcopulatory display follows such copulation attempts.

On 18 June I saw the first successful copulation. Others must have taken place before because, on 14 June, Taylor and Hampson found a nest containing two eggs.

Copulation.—In Rock Ptarmigan, copulation is unhurried. At 00:01 on 18 June, a male and a female flew downslope from camp to some marshy hummocks. On alighting, the female began to feed and the male made the usual flight-song display. Immediately thereafter he approached the female in a courting display with tipped-up tail and neck arched toward the female. The accompanying vocalization seemed to be a modification of the "assurance note" to the female. He moved in a curving path in front of her, trying to keep her from moving away from him. She continued to move away and kept on feeding.

At 00:07, as both birds crouched, I saw another male flying about a quarter of a mile away. They remained crouched until the flying bird had disappeared, then the male rose with an incomplete flight call and disappeared in the direction of the other male. The female remained crouched until 00:18 when her mate returned and displayed. On landing within 25 feet of her, he began the "assurance notes" and fed. The female arose and began feeding.

The male assumed a very upright stance as if alert (Figure 29), and followed her, gradually moving closer until he was eight to 10 inches behind her. As she continued moving on, the male fed briefly, then followed her again. Whenever she paused, he moved closer, sometimes almost touching her tail with his breast. He continued in this following stance with his head tipped down so that he appeared to be "looking down" on the female's back (Figures 30 and 31). As she fed, the female crouched so low that her breast barely cleared the ground, and if the male came too close, she either moved a few inches away or simply raised her head – movements sufficient to halt the male's approach. They repeated these actions continuously until 01:22 when the male moved up to the female as she fed in a depression and almost touched her. She suddenly froze in a lower crouch and slightly moved her wings outward at the shoulders, exposing the white wrists; she again moved a few inches away. The male approached and followed her so closely that her tail projected between his legs and he occasionally stepped on the tip. Finally the female crouched in a small depression, slightly tipped up her head, and moved her wings a bit out at the shoulders.

The male, still holding himself upright, walked over her tail, stepped on her back, and stood there for four seconds before starting treading movements with his feet over her scapulars. He pecked twice toward the female's nape but did not touch or hold her neck feathers. Still in a very upright position he lowered himself on his tarsi so that his body was almost vertical with tail slightly above horizontal and half spread. The feathers on his rump began to rise; he spread his wings widely outward for balance, but did not flutter them. Leaning still farther back he pushed with his tarsi and moved backward until his partly spread tail swept the female's tail aside. As this happened she raised her rear upward so that her tail was up by his breast, and she was resting on her neck and the fore part of her breast.

The male, still upright with wings wide spread and held slightly out from his sides, made side-to-side movements with his tail, and pressed it forcefully against the female as she spread her wings widely and laterally. The male opened his bill but made no sound, extended his neck, and bent slowly forward over her back, tipping up his tail. Then, as if over-balanced, he walked off her back over her right shoulder. Copulation itself took three seconds.

Postcopulatory Display.—With his head and neck still down, tail spread to the fullest and held vertically, and wings bowed outward and spread with their primaries dragging and parallel to the ground, he made a circle three-quarters of the way around the female. As he circled, he turned his tail toward the female, keeping the maximum area of black exposed. With outstretched neck somewhat inflated, he turned his head, with its vivid red combs extending above the crown, toward the female. I heard no sound from his open bill. The female remained crouching with wings still partly spread as the male repeated the display (Plate 1). She then stood up, shook her plumage, preened, shed several white feathers, and ran to the lee of a nearby snowbank and crouched on bare ground at the edge. The male followed her and walking up on the top of the drift, scratched a cup-like depression by crouching down on the snow and kicking it out in a spray behind him. He seemed to rest on his wings while digging. Very soon he scraped a hole from which only his head and tail projected above the snow. Both birds slept in their positions for 15 minutes.

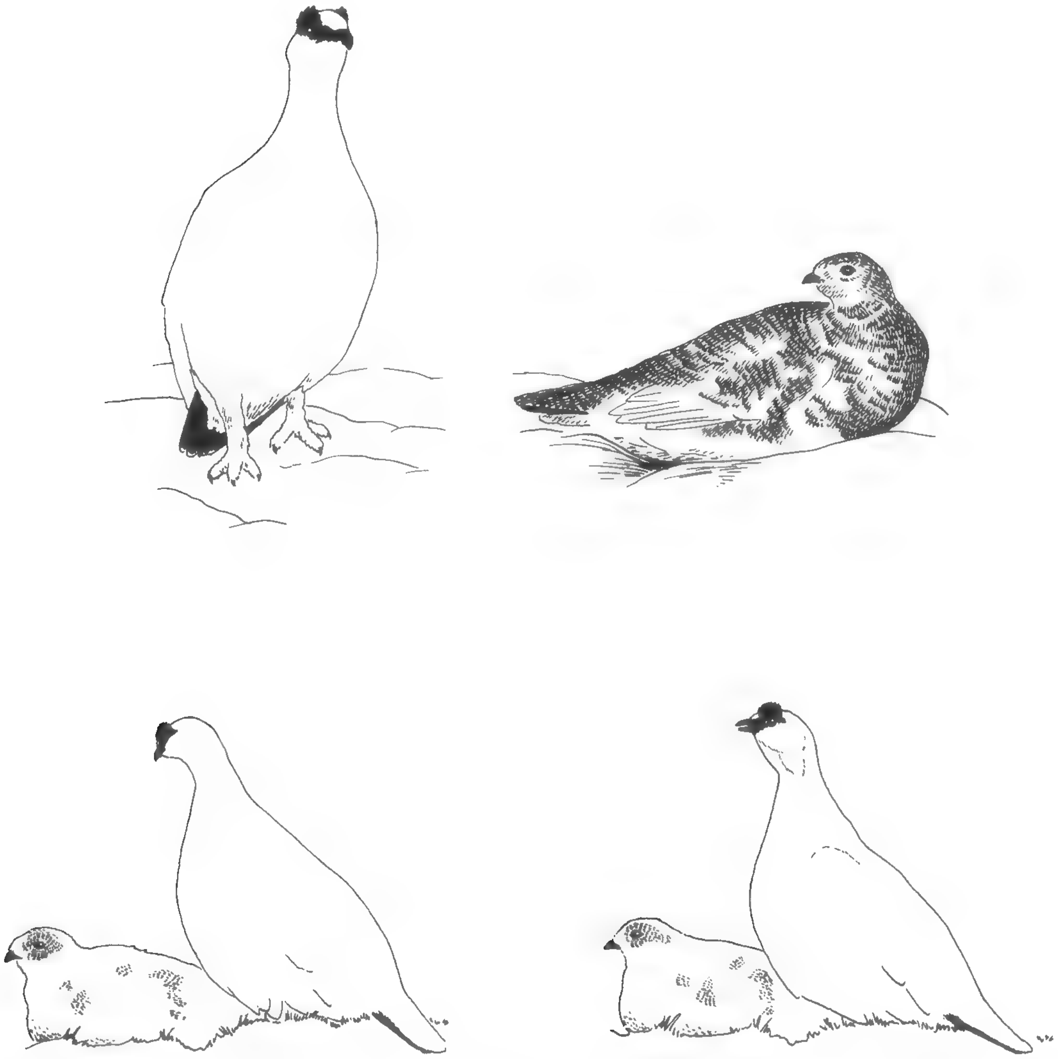
We observed four complete copulations, involving three pairs, in two years. In each case the pattern was basically similar to the foregoing description. In half the cases the female ran from the male before he completed his postcopulatory display; one female did not run. This running behavior is evidently as variable as is the number of times the male circles the female after copulation, but in every case the male walked over the female's right shoulder and circled in front of her toward the left. The male apparently circles twice only if the female remains crouching.

Aggressive Behavior of Females

Females of some grouse exhibit marked aggressive behavior toward other members of their respective species. In Franklin's race of the Spruce Grouse (*C. c. franklinii*), females become so aggressive during the period of egg-laying and before the onset of incubation that they actively seek out and attack any other female in their home range (MacDonald, field notes). Female Rock Ptarmigan are less aggressive, but when a male has more than one mate at one time the females exhibit a hierarchy that seems to reflect the male's preference for them. In every case where I observed encounters between females, the dominant bird assumed a more erect posture, like a male's, and the other assumed the humped-up submissive attitude, typical of females during the early part of the breeding season.

On 10 June, when I placed a mounted female in white plumage where a live female could see it, the first reaction was mild alarm, followed by intense curiosity. She hurried directly to the mounted specimen and moved about in

Plate I. Postcopulatory display of Rock Ptarmigan. In this display the male circles the still crouching female in a way which presents his strikingly contrasting plumage and brilliant combs to the best advantage as he moves around her. The marked sexual difference in the spring molt is apparent, and the cryptic markings of the female blend with background of lichens and willows. Within six weeks the male will have replaced his white plumage with a camouflage of browns. Like other ptarmigan in North America the wings always remain white. Painting by George Miksch Sutton.



Figures 29, 30, and 31. A male Rock Ptarmigan (*top*) assumes an upright position beside the crouching female prior to copulating with her. *Bottom left,* a male in "looking down" posture, straddling the female's tail, just before copulation. *Bottom right,* a male giving alarm call causing the female to crouch. When the female continuously moves away without permitting copulation, the male stands erect and gives an alarm call, halting her movements.

an arc very similar to the male's threatening behavior. Her body was horizontal, her neck was outstretched, her combs showed conspicuously red, and her short tail was tipped up, with the rectrices spread toward the mounted bird. After about one minute she rushed up and pecked the mount on the side of the head near the auriculars — the area where the males attack a mounted male specimen. Several pecks followed, all stabbing blows; she neither held nor pulled out feathers. She used no wing-strokes when she jumped on the mount and knocked it over. This frightened her and she ran away. Then she quickly circled back, trying to attack, but the mount lying on its side alarmed her. I removed this mount and set up a mounted male with large red combs and black in its tail. The female was at once extremely alarmed; she began to circle it with crest erect and both combs and tail concealed. Fifteen minutes later, after making several tentative bowing movements, she flew away.

A week earlier — 5 June — the same female and others had behaved differently toward the same mounted female. They all showed intense interest and a desire to be near it but no evidence of intended attack. The usual behavior was alarm, then a crouch in front of the mount facing it and a head-jerking display like a female Spruce Grouse soliciting copulation. One female while displaying as above suddenly jumped into one of my footprints in the snow and began making jerky and spasmodic movements as if settling on eggs. She uttered a low whining note, also similar to vocalization of female Spruce Grouse. The male responded to the mounted female by rushing up and attacking, pecking at it ineffectually without showing the typical aggressiveness evident in fights between males. He appeared inhibited in his attack until the mounted female fell over; he then jumped on it and hesitatingly pulled feathers out of its cheeks and neck. Several times one male stationed himself between the mounted bird and his mate. When she refused to leave the proximity of the mount, he attacked her and forced her to fly away.

Polygamous Behavior

Rock Ptarmigan males in the high Arctic seem more inclined to polygamy than either Willow Ptarmigan (*Lagopus lagopus*) or White-tailed Ptarmigan (*Lagopus leucurus*). In southwest Greenland, Nicholson (1930) observed a male with two females, one with chicks, on 30 June. The male divided his attention between the two females. Parmelee and MacDonald (1960) noted a male with three females (Figure 32) regularly in a small valley on northern Ellesmere Island from 22 April to 25 June when the male disappeared. Two of these females each produced a brood of chicks.

At Bathurst Island one male had three mates, and all nested successfully within the territory he defended. We found the nests of two of these females before the eggs hatched; the third bird eluded us by her more sedentary habits, and we found her nest, full of empty shells, the following spring. So far as we could determine, none of the six other males we were watching had more than one female. It is not clear why some males are polygamous and others not, but in each case in my experience the male occupied a large territory encompassing what was probably optimum habitat. Multiple mates, control of a large territory, and a high level of display activity must reflect the male's vigor. Certainly his high intensity of behavior, the development of his combs, and his molt pattern were different from all other males.

The hierarchy among this ptarmigan's females seemed related to his preference for each female, a preference that appeared to be based upon the amount of brown plumage present. I assume that early development of brown summer feathers indicates an increase in the female's estrogen, resulting in imminent sexual response. The brownest bird, the male's favorite, was the first female to become attached to the territory; he mated with her first and she laid her first egg before the other two females. He spent more time with this female than any other, and, if she appeared while he was with one of his others, he always joined her. On several occasions he attacked the other female and drove her out of the immediate area. I interpret this behavior to mean that monogamy is the normal mating relation in Rock Ptarmigan.

In addition, our experiments with mounted females suggest that territorial males are more sexually oriented toward females with piebald plumage than to whiter females — that is, males preferred females with more brown feathers. A male whose mate was piebald in color behaved aggressively toward a pure white mounted female. When I painted the plumage of the mounted female darker and added mottled paper "feathers" to the back and rump, giving the mount a more advanced plumage than his mate's, he began courting it and flew at his whiter female, driving her away.

When the polygamous male directed his attentions from one female to another nearby, the deserted female attempted to divert the male by placing herself in front of him and by soliciting him sexually but not allowing him to copulate. Watson and Jenkins (1964) recorded similar behavior in Red Grouse (*Lagopus scoticus*). In each case, the female distracted the male's attention from her rival female without displaying any aggression. The polygamous male, forced to divide his time between females and to maintain constant surveillance of a greater area of the territory, is subjected to greater stress than the monogamous male. This hyperactivity that makes him more conspicuous than the monogamous male may increase his chances of being killed by a predator, and thus it may function as a selective factor against polygamy.

Excerpts from my notes of 19 June illustrate the activity of a male with two females.

08:12. Female running along slope above river terrace; very hunched, dumpy appearance typical of female just off the nest. Still has white areas on cheeks, neck, upper breast, and sides. Back, scapulars, wing coverts, rump, and central tail coverts brown. Flew 200 yards, landed on a moist slope near patch of dirty snow and fed.

08:20. Feeding interspersed with running about 20 to 40 feet with neck pulled in on shoulders and tail down.

09:12. Male flew over and landed on the ridge but apparently did not see female beside a hummock where she had been sleeping and preening since 08.26.

09:15. Female feeding and moving up hill, out of sight of male.

09:25. Female moving toward male on hummock 150 yards away; now visible to him. Flew toward her, dipped down directly over her head, then soared up into the wind in a high Flight-song. Landed 60 feet away, displayed, and approached her with head down and tail spread obliquely toward her. She allowed him to approach within inches of her and to follow her closely. Gradually she allowed him to stand briefly with his breast over her rump and her tail extending between his legs.

09:50. Copulation, postcopulatory display. Female ran about 10 feet away, fluffing plumage and shaking wings; male ignored her and moved away.

10:00. Pair feeding 12 feet apart.

10:07. Male sleeping on top of hummock; female crouching behind same hummock, sleeping, preening.

10:30. Male feeding on buds, twigs of willow, and flower buds of purple saxifrage.

10:40. Male sitting on hummock, 100 feet from female which has not moved since 10:07.

12:35. Both birds moved to shelter of snow drifts. Male sitting on clean snow, female on dirty snow.

12:51. Female feeding, moving away from male.

13:13. Male fed; then approached female in an arc—head down, partly spread tail tilted toward her. Female approaching same locality as at 08.12. Male still displaying and approaching female; drove her toward hummocky tundra with small depressions. Female allowed him to follow closely and crouched in a depression when he stepped on her tail. Twice she crouched and he put one foot on her back before she moved forward.

13:41. Same following behavior. Suddenly male became alert, craned neck, made ratchet alarm note, and female flattened into a depression. Male also crouched, then stood up as a female in brown plumage landed about 70 feet away and flattened herself in a depression between hummocks.

13:55. Male ran about 10 feet with neck outstretched, tail horizontal and partly spread, and wings drooping, then ran back toward whiter female. When he was about six feet from her, she jumped up and ran in a zigzag course through the depressions, dragging her wings and mewing. As the male came closer to her she crouched momentarily, then ran again. Five times the male attempted to step on her back, but she wiggled from under him and crouched in another spot a foot away. Finally, the male ran up to the crouching female and pecked her sharply on her head. She jumped up and ran off with him chasing her—both going much faster than before. After running 70 to 80 feet in a turning and twisting path, the male suddenly flew at her, struck her solidly with his body, and, at the same time, pecked her on the neck. He attacked a second time and pulled a bill full of brown and white feathers out of her back and scapulars. She flew off uphill with the male in pursuit, both in an erratic, twisting flight, and disappeared over the ridge at 14:05.

14:10. Male returned, soared up to about 100 feet in a magnificent Flight-song and sang twice before alighting 35 feet from the brown female still crouching in a hollow among the hummocks. He approached and began courting her; she stood up and began to feed with him following her very closely in the precopulatory attitude. She seemed ready to copulate when both birds suddenly crouched, and the whiter female returned, landed about 75 feet away, and huddled in a small hollow, mewing. The male ran toward her with tail raised and partly spread and head low; then he flew to her, landing without a display in a position from which he could not see the brown female. He turned and ran back to the top of the small rise where he could see the brown female still crouching among the hummocks. Again he ran back to the white female and chased her for more than 100 yards in an erratic pattern uphill toward the soggy hummocks below a large snow drift, but he did not attack her. He simply chased her with only about 18 inches separating them. Periodically she swerved suddenly to the side and huddled in a depression. At

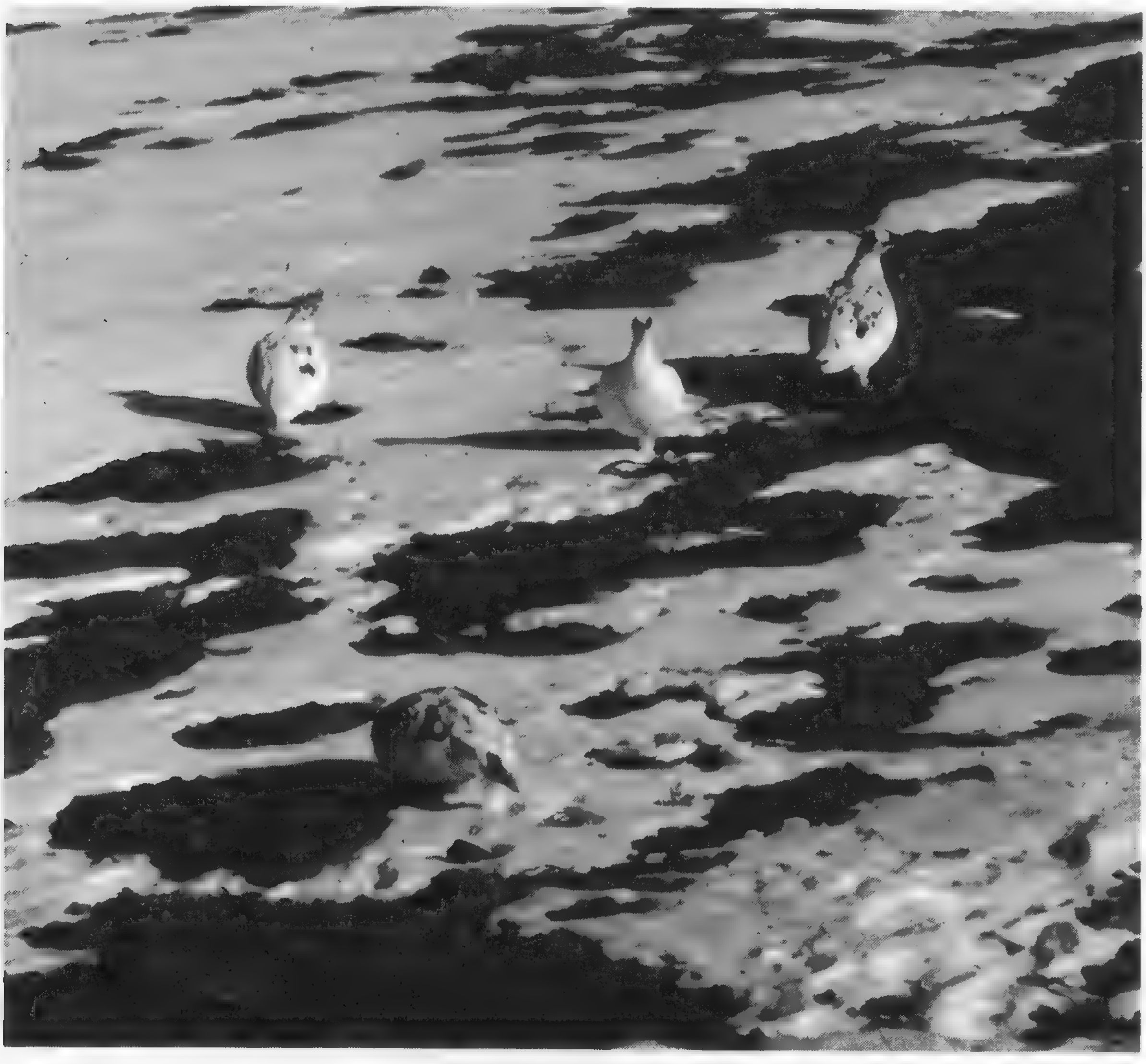


Figure 32. Polygamy occurs occasionally in Rock Ptarmigan. Here a male and three females feed quietly on buds and twigs of arctic willow. Two of these females nested in the male's territory at Eureka on Ellesmere Island.

the male's approach she ran and the chase continued. Finally, she crouched in another depression and wriggled about as if settling on eggs (Figure 33). The male immediately stopped chasing, looked at her briefly, finally ran a few steps downslope and flew to the brown female without any flight-song display.

14:20. Began following brown female and then attempted to halt her course away from the hummocky ground. She continued downhill to the river bank and sat on the bare ground in the lee of a large snowdrift where she ate pieces of broken clamshells. White female again moving downhill. Male, sheltered behind a rock on edge of bank immediately above the brown female, then flew off. No vocalization.

14:24. Male returned, high Flight-song over brown female which began feeding. White female began moving and feeding toward him; because of a low ridge she could not see brown female. White female started making mewing notes and when she reached the ridge top and could see the brown female, she crouched and became silent. The brown female continuing uphill ignored the pale one. The male, very agitated, started displaying to white female. As the brown one partly crouched, he again ran at the white bird which moved off as before—crouching, dragging her wings, mewing, and keeping about three feet ahead of him. After running about 150 to 200 yards downhill, she crouched in a depression as if settling on eggs. The male walked up in the precopulatory attitude and stood beside her, looking down on her back; she began making side-to-side movements as if rolling eggs. Finally she closed her eyes. After three seconds the male turned aside and started uphill feeding.

15:35. Male sitting on hummock, brown female feeding 100 feet away, and white female still crouching in the same depression.

Vocalizations

The vocal sounds of Rock Ptarmigan almost defy description and do not lend themselves to onomatopoeic or phonetical rendition. The territorial male has a repertoire of at least six distinct vocalizations, all of which are variations of a predominantly low frequency pulse-burst of cyclic clicks. They resemble, if one ignores the frequency response, the sound produced by pulling a stick across the slats of a picket fence at varying speeds.

The female produces at least three vocalizations, similar to the whining and clucking notes of other female grouse. The third utterance is a high-pitched screech, which I did not record; I heard this only twice from two separate females. In each case the bird, not with her mate, walked up on a small prominence, stood very upright as if alarmed, and gave the shrill call which sounded something like *e-e-e-yu-u-uck, e-e-e-yow uck.*

The vocal apparatus of Rock Ptarmigan may be unique among tetraonids, except possibly for the Willow Ptarmigan and the Red Grouse. While vocalizing, the male inflates his esophagus, as do most of the grouse species during courtship. In addition, he also uses an inflatable membranous outpocketing of the dorsal surface of the trachea (Figure 34), a structure, about the size of a small walnut, that lies just below the larynx where the tracheal rings are incomplete on both their dorsal and ventral surfaces for a short distance. In this area the ventral surfaces of the rings are joined by a tough membrane which functions as a hinge, allowing the rings to extend laterally and to flatten their curvature when the dorsal membrane is inflated. I shall discuss this structure and its use in sound production in a separate paper.

Incubation and Care of the Young

We found four nests within a two-mile radius of the camp at Bathurst Island. A fifth one we found the following year with the empty shells, still in the nest-cup, bleached and conspicuous. Three of these females were mated to one male; they laid a total of 25 eggs; and all hatched except two. Hampson and Taylor found the first nest on 14 June by watching the female until she returned to lay in it. This technique works best while the ground is still only partly free of snow and one can see from a distance the progress of the female from one bare patch to another. When most of the snow is gone, the females spend most of their time incubating and, because their plumage is mainly brown at this time, they are difficult to detect, easily eluding a human observer by crouching and moving in depressions.

The males frequently escort laying or incubating females back to their nests. In each case the male seemed to "know" the location of the nest. He may accompany the female in flight to the nest area, but not directly to the nest. Parmelee (1968, field notes) noted that the male frequently gave flight-song displays over the nest site, usually alighting 30 feet or more away. One male landed within 10 feet of the nest when a Long-tailed Jaeger (*Stercorarius longicaudus*) flew over it while the female crouched on the eggs. On other occasions, the female walked to the nest with the male following about 10 or 15 feet behind. While the female settled on the eggs facing the wind, the male stood about six feet away for five minutes, then flew off and performed a flight-song.

All nests were in depressions where the females had made a shallow scrape. During the laying of the first three or four eggs, the nest scrape gives little indication of being used, but the subsequent movements of the female, throughout the egg-laying and incubation periods, gradually enlarge and deepen it.

In the early stages of egg-laying when the air temperature is close to freezing and the ground newly thawed, the female carefully protects the eggs from the cold by covering them with plant material before she leaves the nest. On 19 June, one nest was covered with fresh snow when the female returned to lay her sixth egg. In addition to protecting the eggs from the elements, the covering must reduce the probability of the nest being found by avian predators. Although covering the eggs may protect them from birds, it apparently does not handicap the arctic fox (*Alopex lagopus*).

Fresh Rock Ptarmigan eggs, rich cinnamon-red with deep chestnut-brown markings and blotches, are more conspicuous than later when incubation is under way and their beautiful cinnamon ground-color fades to drab buff and the spots and splotches deepen to almost black. Curiously, when the female leaves her completed clutch to feed, she does not cover the eggs. Several times we saw Long-tailed Jaegers flying over nests of uncovered eggs, but they did not see them. One jaeger dipped down over the head of a female Rock Ptarmigan returning to her nest to lay her third egg. She stopped, stood erect, and raised and spread her tail. The jaeger continued on its way.

When a female returns to her nest to lay, she may walk or fly to the nest area where she feeds in an agitated manner. She keeps her head and tail low, and she adopts a hunched appearance concealing her white underparts. She punctuates her hurried feeding by runs which bring her close to the nest site. Then with a last quick run she settles on the nest with periodic twisting and turning. During the actual laying of an egg, she stands in the nest with the

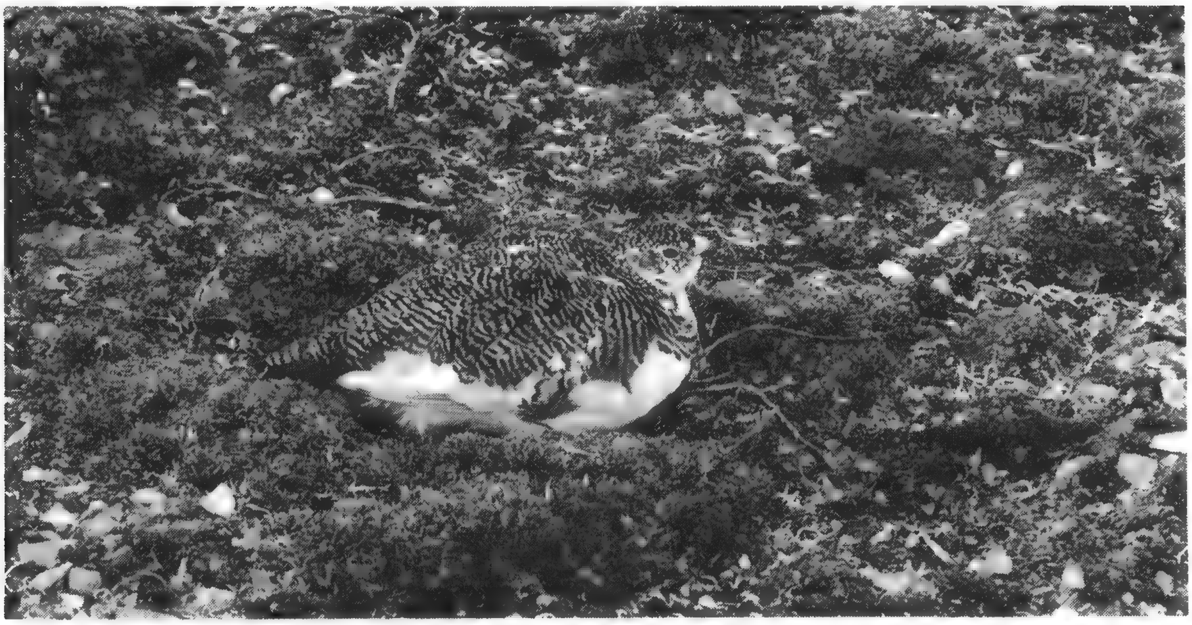


Figure 33. A female crouching in a hollow fringed with *Dryas* and arctic willow. She was feigning incubation, trying to attract a male which, after following her, has left to join his preferred mate, newly arrived in the area.

front part of her body raised, neck pulled down on her shoulders, and her tail lowered. After the egg is laid and the female rests briefly, still sitting on the eggs, she begins pecking at adjacent plant materials — mosses, lichens, grasses, willow leaves, twigs, and anything else within reach including pebbles. She picks up this material and places it in the nest on each side of her. Invariably she turns back her head to one side or the other to deposit the material (Parmelee, 1968 field notes) but apparently does not place any in front of her. She may continue pecking movements for more than half an hour. Sometimes she moves off the nest, gathers materials, and deposits them on either side as if she were on the nest, so that when she leaves the nest, the eggs are usually completely concealed. If a part of the covering blows off during windy weather, the eggs remain uncovered until the female returns to lay the next egg — about 24 hours later. As the clutch nears completion she spends less and less time picking vegetation and covering the eggs until, during incubation, she leaves them completely uncovered. While incubating, the female eats any white feathers, even those up to four inches in length, which are evident around the edge of the nest.

Watson and Jenkins (1964) noted that the female Red Grouse covers her eggs with vegetation when she leaves the nest, particularly as the clutch nears completion. White-tailed Ptarmigan, when laying, cover their nests with vegetation before leaving (Bradbury, 1915). Schmidt (1969), who also found a nest of that species with the eggs partly covered, was unable to decide whether this is typical.

All female Rock Ptarmigan at Bathurst Island whose nests we found were closely synchronized in start of nesting and egg-laying. One female may have laid a second clutch of eggs; our only evidence was that her eggs hatched nine days later than the others.

The females incubate steadily for long periods, possibly leaving the nest to feed only at 12-hour intervals. During incubation the male usually remains at an observation post with a view of the nest site. When the female leaves the nest, the male often accompanies her to a feeding area. Stimulated by her appearance, he may give a Flight-song or attempt courtship. She ignores him. If the male is absent when the female leaves the nest, she may walk a short distance and fly, or simply take a few steps and fly low, following the contour of the ground, to a feeding area. Rapid and shallow strokes, alternating with short periods of sailing, make the bird's white wings during this semi-fluttering flight seem to twinkle against the bare slopes in a manner that is very conspicuous, even to a human at a distance. The termination of this flight is even more conspicuous. As she alights, she may rise slightly and, while rapidly fluttering, drop to the ground. Occasionally she flies 20 or 30 feet farther and repeats the fluttering maneuver, a behavior that seems to announce her presence to the male which flies to join her and maintains a constant watch while she feeds. He may remain with her until she finishes and then escort her back to the nest area, or he may fly off and leave her. From my small amount of data, it appears that a lack of interest in the female at this time signals the male's imminent desertion of the territory and his move to some sheltered hummocky gully to molt.

The incubation period of Rock Ptarmigan is 21 days according to Salomonsen (1950–1951). In a clutch of 10 eggs at Bathurst Island the tenth egg failed to hatch. This meant that the incubation period could not be determined in the traditional manner. The female, however, commenced "what appeared to be" steady incubation with the laying of the *ninth* egg which gave an incubation period of 20 days, 14 hours (±3 hours) for that egg (Parmelee, 1968 field notes). In his nest study, Parmelee recorded the first slight crack (star) in one egg at 06:30 on 11 July. At 12:00 there was little change, but by 18:15 there were three chicks, two dry and one wet, in the nest and by 19:30 four young were hatched; five of the remaining six eggs were pipped, including the ninth egg, but not the tenth. By 21:15, nine young had hatched and five were still wet. By 04:45 on 12 July, the last egg still had not hatched; the female brooded the young in the nest, but they were very active and were able to walk and run well. One chick pecked vigorously at purple saxifrage near the nest. At 06:15, the female brooded nine chicks five feet from the nest where the tenth egg lay, still unhatched. They had moved 200 feet from the nest by 09:15 and the female brooded them all. On 24 July, eight of the original nine young remained; they could fly too well to be caught by hand.

Salomonsen (1950–1951) states that a less than 10-day-old chick can fly "up to 10–15 m"; Parmelee and I (1960) at Eureka watched a chick, known to be approximately 15 days and six hours old, that could fly only about eight feet. Throughout the remainder of the season (until 12 August) this female and her chicks remained within a radius of about one mile of the nest site. We noted a similar limited range of a marked female with a brood at Eureka in 1955 (Parmelee and MacDonald, 1960).

Protection of Nest and Young.—Female Rock Ptarmigan sit very closely on their nests and rely upon their cryptic coloration to conceal them. One may lift some females gently from the nest or reach under them to remove eggs for inspection. Once flushed from the eggs, most females exhibit strong protective behavior and well-developed distraction displays.

An incubating female, disturbed on the nest, hisses loudly and sometimes pecks vigorously at a hand touching her. Following this, she suddently leaps from the nest and scuttles about erratically in a crouched position. She lowers her wings and drags her partly spread white primaries and tail on the ground. In high intensity, she may flap the wings against the ground. The movement of this plumage over the ground combines with hissings to produce a surprisingly startling, hollow rasping sound that may also be accompanied by plaintive whining notes. This distraction display — "injury feigning" — is interspersed with sudden stops with wings held away from the body and the spread primaries resting on the ground with the wings trembling violently. As the display continues, this shivering gradually diminishes and finally disappears completely. At this point, the female may stop displaying and walk away in a rather alert posture. If one walks toward her, the display begins anew at a lower intensity, and she trails herself away from the nest, continuing to "lead" one away. I followed one female in this fashion for 300 feet before she finally flew away. A female places herself directly in one's path during a distraction display, and as long as one follows, she moves straight away; if one turns aside from her direction, she immediately alters her course so she is again directly in one's path.

When the young hatch and are still unable to fly, the female becomes particularly aggressive. Some females fly into the face of anyone close to the chicks, especially if a captured chick peeps in distress.

Male Rock Ptarmigan at Bathurst Island seemed to have little to do with the females after the young hatch. Salomonsen's statement (1950–1951) that males desert the females slightly before hatching applies to the majority of

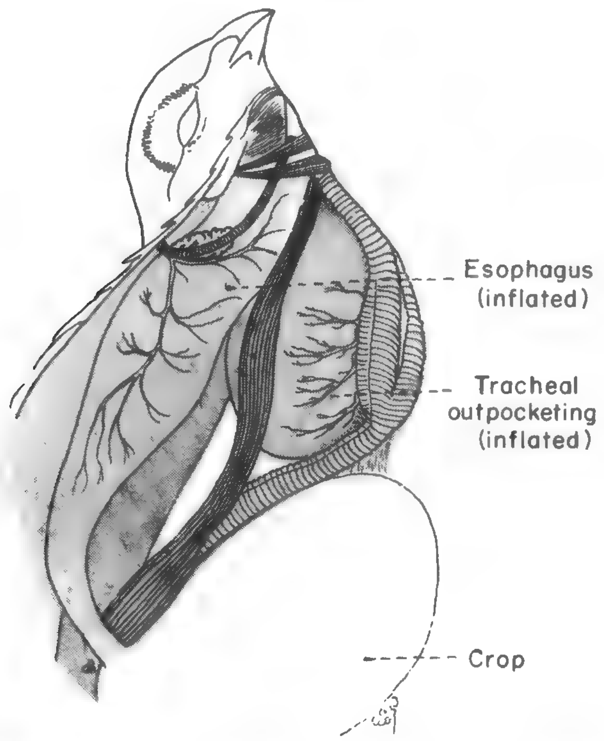


Figure 34. The inflatable portion in the trachea of a male Rock Ptarmigan. The portion of the trachea below the larynx is stretched to the maximum, and the esophagus is also inflated.

Bathurst Island birds and to those at Ellesmere Island (Parmelee and MacDonald, 1960). Taylor (1968, field notes), however, observed a female with chicks at Bathurst being harassed by a Snowy Owl (*Nyctea scandiaca*). The owl, taking short hopping flights on the ground within eight feet of the adult, was apparently chasing the chicks which, though able to fly, did not. The owl flew off when Taylor approached it within 75 to 100 yards and, as it flew away, a male Rock Ptarmigan suddenly appeared and flew paralleling it to a ridge where the owl landed and the ptarmigan gave a weak flight-song. The male soon joined the female.

At Prince Patrick Island, male Rock Ptarmigan are much more protective and exhibit marked anxiety when anything disturbs the incubating female at the nest, or threatens the newly hatched young. I saw males drive Long-tailed Jaegers from the nest area and from females with broods (MacDonald, 1952). In one case a Long-tailed Jaeger swooped down and caught a small flightless chick in spite of the female's display. The male, typically nearby, flew down and forced the jaeger to leave, but still carrying the struggling and crying chick. The male pursued it in swerving flight with great agility, soon overtaking it and striking it heavily with his breast. The impact caused the jaeger to drop the prey. Undisturbed, the jaeger picked up the chick, apparently dead, and took off; the male ptarmigan returned to his observation post. Another male accompanied a female with four half-grown young on 4 August (Parmelee, 1968 field notes).

A male Rock Ptarmigan at Ellef Ringnes Island successfully lured a husky pup away from the nest territory by a series of short flight-song displays and ground displays (MacDonald, 1959).

Plumage Change

Rock Ptarmigan in the Far North have a marked sexual difference in the spring molt. The females attain their brown, cryptically marked summer plumage about the same time they complete their clutch of eggs and the ground is half free of snow. The male remains conspicuously white long after much of the snow in his territory has melted. Through periodic dusting, this plumage becomes increasingly dirty with some males showing a marked variation in the intensity of the staining.

Salomonsen (1950–1951) states that the initiation of the molt in the male is suppressed by the neutralizing effect of the testicular hormone on the hormone that stimulates feather growth. This would also explain the variation in timing of the initiation of plumage change, evident in individuals. At Bathurst we conducted a simple experiment, perhaps too limited to permit a positive statement, but nevertheless it appears to support Salomonsen's view.

On 23 June, Taylor succeeded in snaring the male occupant of a large territory near camp. This bird was still completely white except for a few brown feathers on his crown, neck, and shoulders. His combs were brilliant and fleshy, with a well-developed fringe of papillae along the top. We injected him, subcutaneously at the base of his neck, with 1.2 cc of aqueous suspension of testosterone (25 mg/cc, Paul Maney Laboratories, Toronto) and an additional 0.8 cc of sterile saline to equal 2.0 cc, sprayed his left wing with

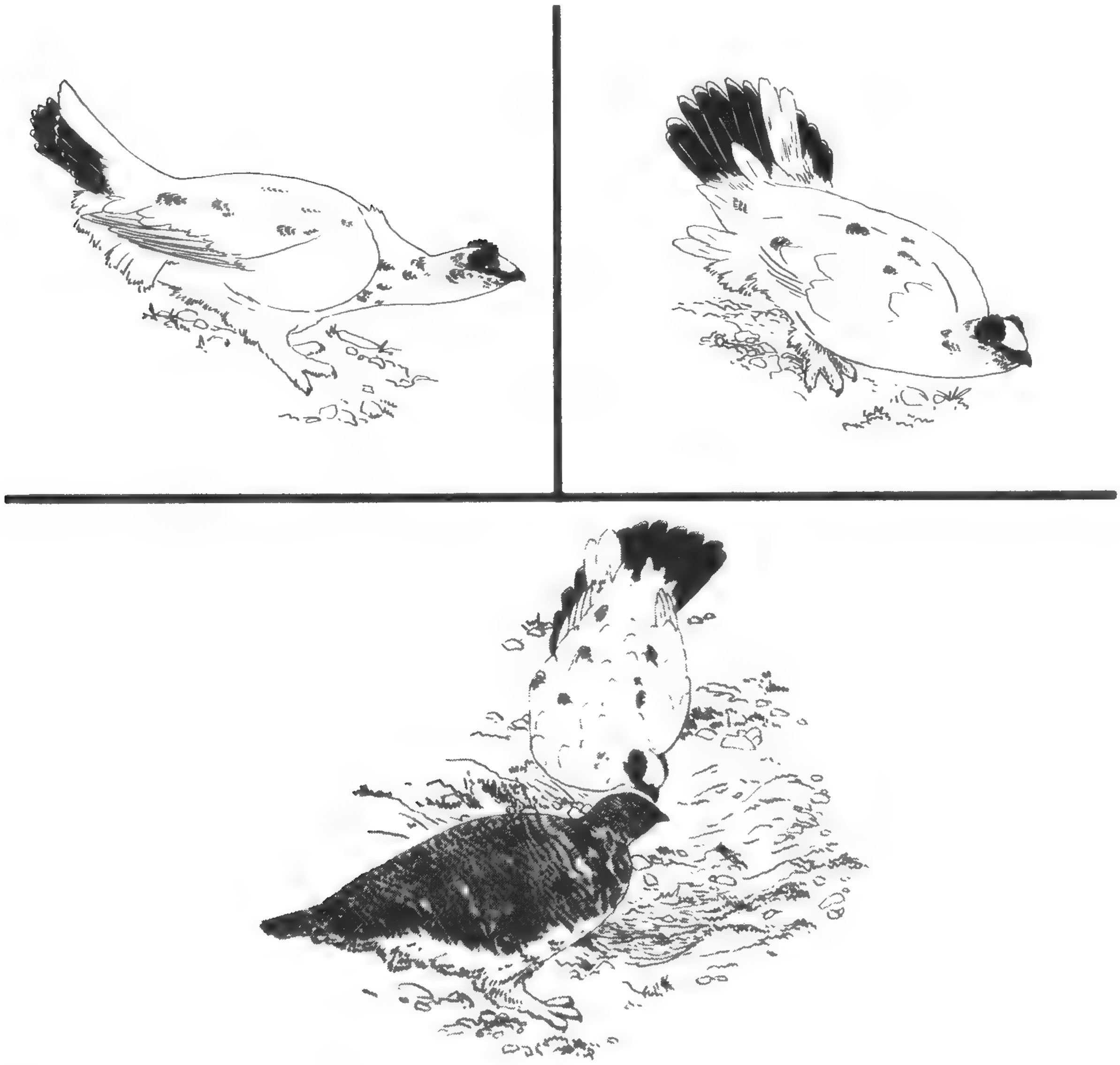


Figure 35. Behavior and plumage of a male Rock Ptarmigan injected with testosterone. He is still almost white, while all the other males are completely brown. Here he courts a female which has left her nest and eggs to feed. Crouching at the edge of a depression, he tries to induce her to enter and crouch for copulation.

fluorescent red paint, and released him. Subdued at first, he gave no displays, but, within 12 hours, his behavior appeared normal. Gradually his display activity increased to about the same level as we had observed during the late pair-bond period. By 8 July, when some adjacent males were almost completely brown and others were molting extensively, he was whiter than any of them. This male, known to have mated with three females nesting in his territory, courted each persistently whenever she left her nest to feed (Figure 35). His Flight-songs were spectacular in height, frequently reaching an estimated 250 feet, and he sang two, three, or even four times before alighting. On 12 July, he chased a female two miles west of his usual area of activity. He ignored a female accompanied by young and devoted himself to escorting the incubating female whose young hatched about 22 July. We have no evidence that he, or any other male, continued to court any female when she had returned to the nest and settled on the eggs.

On 20 July, his plumage was about one-third brown. The dark feathers were scattered uniformly over his body, though his back appeared predominantly whitish and the remaining white plumage was very dirty and worn.

His combs were still large and bright red, with the erectile fringe still prominent. As I approached to within 30 feet of him, he gave two aggressive, challenging vocalizations. With binoculars, I could determine that most of the brown feathers had the delicate pepper-and-salt pattern, or fine vermiculations characteristic of the late summer plumage. We never saw this bird again although we searched the surrounding terrain until mid-August. I suspect his hyperactivity, extended flights, and very high Flight-songs attracted the fatal attention of an avian predator. This single experiment, whether or not it substantiates Salomonsen's views, does suggest that we need more work, under controlled conditions, to determine the role of hormones in the development of brown plumage in breeding Rock Ptarmigan.

Summary

This descriptive paper on a continuing study of Rock Ptarmigan (*Lagopus mutus*) at Bathurst Island, Northwest Territories, Canada, covers their behavior and life history and discusses habitat preferences during most of two breeding seasons.

In spring the males develop above each eye conspicuous red combs that function as visual signals in sexual identification, and in all encounters with fellow members of their species as well as with other animals. The size and intensity of color of the combs indicate the individual's aggressiveness and reflect the amount of gonadal hormone in the blood. I have described these display structures in detail. The black tail of both sexes and the black face mask of the male are also important in displays.

Males arrive on the breeding grounds and are joined by females while the land is still wintery. Typical flock behavior prevails until late May when the increasing aggressive behavior of the males causes the groups to disperse and females to establish themselves in a breeding habitat controlled by a single male. A female soon becomes attached to specific feeding and sheltering spots in his territory, and the male, tending to center his display activity in these areas, follows her in flight. She quickly adopts a more submissive attitude, begins to rely on the male's watchfulness and warning calls, becomes more inclined to hide than fly, and begins molting. When the male flies off to encounter another male and leaves the female hiding in his territory, the pair-bond is secure.

In this high arctic population, territories are large and without fixed boundaries, although adjacent males engage in actual and ritual fighting at specific places. I have described the male's Flight-songs, to which other males respond, and considered the use of the tail as a planing surface in aerial displays.

During courtship the male follows the female in a horizontal position, displaying his combs and black tail, and tries to induce her to crouch in a depression for copulation. In the precopulatory posture, the male stands upright and follows the female very closely. Copulation is unhurried and followed by a postcopulatory display.

Polygamy occurs periodically, and there seems to be a hierarchy among females of a polygamous male, based on his preference for an individual

female and the development of her brown plumage. Males are very vocal during the first half of the breeding season. We recognized at least six different calls, all modified from a basic pattern of clicks and varied to suit the occasion by the pulse-repetition frequency. Females have at least three vocalizations; none resembles the calls of males.

Egg-laying begins at the end of the second week of June and, while the clutch is incomplete, the female covers the eggs. The female alone incubates for about 21 days. Males, aware of the location of the nest, escort the female from it to the feeding ground and back. Most Bathurst Island males leave their territories and mates before the young hatch, and those which remain appear to have little to do in protecting the young from predators.

An injection of one male with testosterone at the onset of the summer molt increased and prolonged his territorial advertisement and display, and apparently suppressed the normal molt pattern.

Acknowledgments

This paper represents a progress report on one of a series of continuing research projects at Bathurst Island, made possible through an effort between the Canadian National Museum of Natural Sciences and the Canadian Polar Continental Shelf Project, Department of Energy, Mines and Resources. I gratefully acknowledge Dr. E. F. Roots, Coordinator of C.P.C.S.P., and Mr. F. P. Hunt for their support and interest in our research program there.

During the two summers in the Arctic, I enjoyed the cooperation and assistance of colleagues and students who, in addition to their own work, found time to make useful observations for me on Rock Ptarmigan.

Dr. C. G. Hampson, Mr. Philip S. Taylor, Mr. David R. Gray, and Mr. Pierre Lamothe, all from the University of Alberta in Edmonton, also kindly loaned the photographs credited to them in this paper. I am especially grateful to Dr. David F. Parmelee, Kansas State Teachers College in Emporia, for the use of one photograph and for his meticulously prepared field notes on Rock Ptarmigan, and to Dr. George Miksch Sutton, University of Oklahoma in Norman, for his remarkable ability to use one of my hastily prepared field sketches and a freshly collected specimen in producing the beautiful color plate that enhances this paper.

I also express my thanks to Mr. J. W. Van Alstine, Chief of Technical Services at this Museum, for the construction of the collapsible supports for my observation blinds; to Mr. Don Pentz, Museum artist, who prepared the fine line drawings of displays and maps; and to Mr. David C. McMillan, Carleton University, who prepared the anatomical drawings.

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All drawings of displays appearing in this paper are from photographs. The original anatomical drawing is exactly life size and the size of all structures is based upon actual measurements.

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NATIONAL MUSEUMS OF CANADA, OTTAWA

THE EASTERN BLUEBIRD: ITS BREEDING SEASON, CLUTCH SIZE, AND NESTING SUCCESS

DAVID B. PEAKALL

The Eastern Bluebird (*Sialia sialis*), a colorful and favorite species, nests in eastern North America and migrates to the southern United States for the winter. Almost everyone, regardless of his interest in birds as a whole, is familiar with the bluebird and many are concerned because its numbers have decreased greatly in the past two or three decades. Thousands of birdboxes have been erected to accommodate it. The major scientific studies on the Eastern Bluebird include those by Laskey (1939; 1940; 1943), Low (1933), and Thomas (1946).

The Cornell Laboratory of Ornithology established the North American Nest-record Card Program for the purpose of gathering data on the nesting of birds in conterminous United States. This study of the Eastern Bluebird represents the first major analysis of the nest-record cards in this program and includes data from 8,108 nests of the Eastern Bluebird. Even though this analysis is based on more data than any other comparable study of a single species, the records from some areas are still rather sparse because of the broad geographical area included in the bluebird's nesting range. I have divided this range into 15 areas (Table 1).

A History of Nest-record Card Programs

Since this is the first major analysis in North America based on nest-record cards, it seems appropriate to give a brief history of other programs. In 1939, James Fisher and Sir Julian Huxley, working in Britain through the British Trust for Ornithology, initiated the first nest-record card program. Its present file of about 238,000 cards increases by more than 20,000 cards yearly – 25,610 in 1967 (Mayer-Gross, 1970) – and has proved to be very useful. Almost every major paper on breeding biology of birds in Great Britain includes data, at least in part, from this program. Burton and Mayer-Gross (1965) list publications that depended wholly or partly on it for nesting data. The success of the English program stimulated similar programs in other parts of Europe and in South Africa, Australia, and North America.

In North America a number of nest-record card programs began on a regional basis often with a specific purpose. The Detroit Audubon Society used data from a program, initiated in 1945, in compiling the "Birds of the Detroit-Windsor Area" (Kelley, *et al.*, 1963). A similar program in Kansas provided data for Richard F. Johnston's "Breeding Birds of Kansas" (1964). Programs in Canada began with the Pacific Nest Record Scheme in 1955; coverage in that country was complete when the Maritime Provinces started a Nest Record Scheme in 1960.

The North American Nest-record Card Program began at Cornell University on a local basis in 1963, supported by a modest sum donated annually by the Onondaga Audubon Society. It became a nation-wide program in 1965 with the Cornell Laboratory of Ornithology serving as a distributor and collector of cards and as a central clearing house for the analysis of records. In 1968, we entered the magical world of *the machine* and began computerizing the program.

We depend on and appreciate the untiring efforts of the regional organizers who distribute the cards through the regional centers, and the observers who faithfully fill out a card for each nest found. Several visits to one nest increases the value of the card. The distribution of cards through regional centers has two distinct advantages: first, the local organizer is more likely to know of possible observers in his area and can judge the competence of each; and second, it reduces the mailing and communication procedures. See Peakall (1969) for a list of regional centers.

At first glance the format of the card (Figures 1 and 2) may seem complicated. It is really quite simple if one follows the directions step by step. In the end, each card contains a maximum amount of information, packed in the smallest possible space and so organized that it can be edited easily and transferred directly on to IBM punch cards. In designing this card we had the advice of Chandler S. Robbins, U. S. Fish and Wildlife Service, and many useful suggestions from the organizers of the regional programs. See the Appendix to this article for editing procedures.

Geographical Distribution of Records

The U. S. Fish and Wildlife Service conducts annual surveys of breeding birds throughout the United States (Robbins and Van Velzen, 1969). The map, Figure 3, based on data from the Breeding Bird Survey of 1968, shows the relative abundance of the Eastern Bluebird throughout its breeding range and provides much more information than a general range map. The areas with the highest density, the two top categories, all lie in a broad, but irregular, belt from Oklahoma through southern Missouri, northern Arkansas, Kentucky, and Tennessee to West Virginia and southern Ohio.

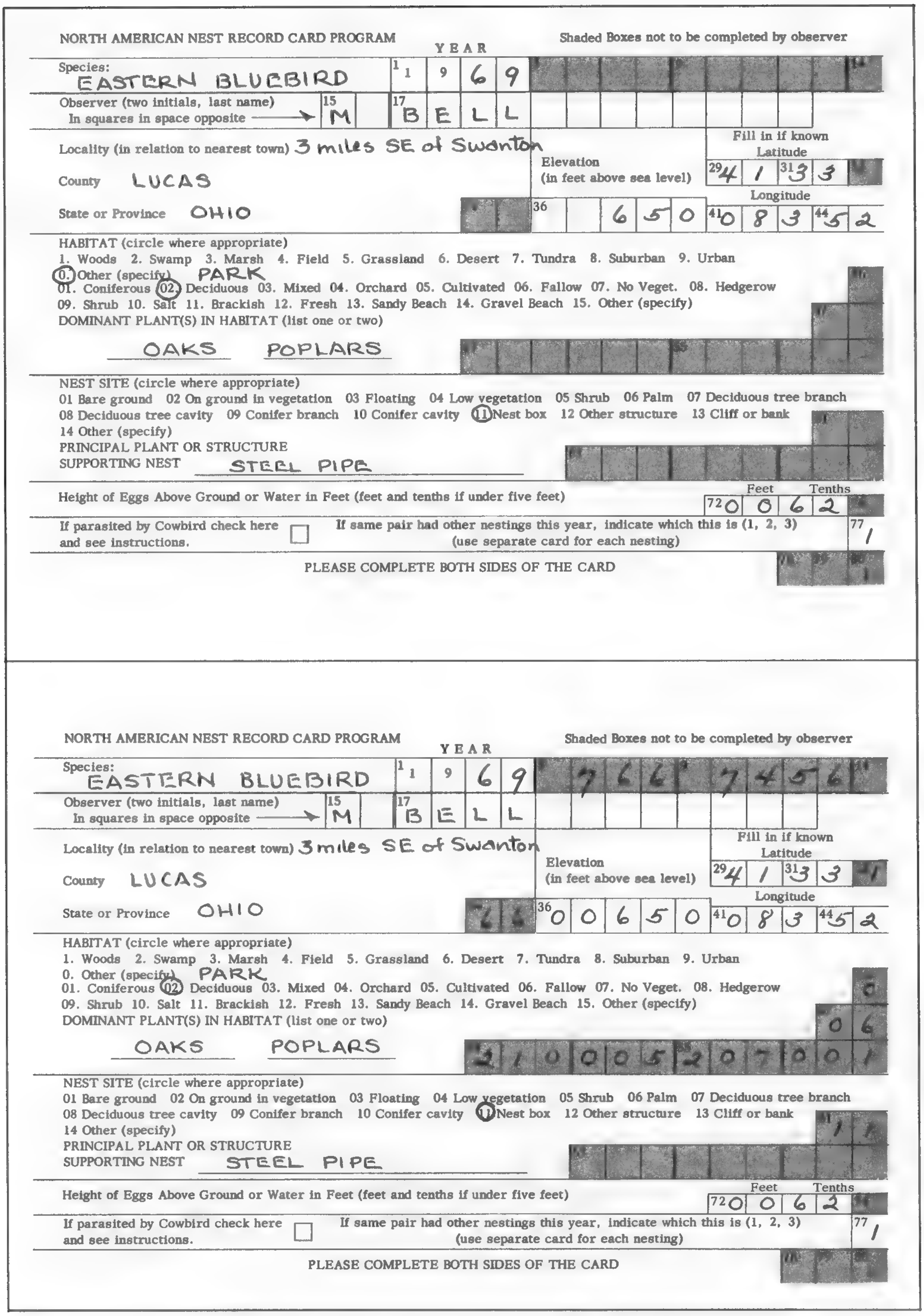
The Nest-record Card Program shows the breeding success each year; the Breeding Bird Survey indicates the changes in population density from year to year. Thus, the two programs complement each other, and, by using both, one can determine whether or not a change in the population of a species is correlated with a change in its productivity.

In Great Britain, Ginn (1969), who analyzed the annual banding and nest-record card totals as indicators of bird population levels, concluded that

TABLE 1

Number of Nest-record Cards on the Eastern Bluebird Available for Analysis, Grouped in Geographical Areas Used in the Analysis

Area number and locality	*Prior to 1964*	*1964*	*1965*	*1966*	*1967*	*1968*	*1969*	*Total*
1. Ontario	38	10	8	15	7	22	0	100
Quebec	6	7	13	11	9	5	0	51
Sub-total	44	17	21	26	16	27	0	151
2. Connecticut	0	0	11	11	10	11	21	64
Maine	0	0	2	1	0	0	0	3
Massachusetts	9	5	9	23	2	0	0	48
New Hampshire	3	0	0	2	2	0	0	7
Vermont	0	0	7	3	4	3	0	17
Sub-total	12	5	29	40	18	14	21	139
3. New York	139	207	289	234	204	176	65	1,314
4. Pennsylvania	417	165	199	262	383	441	362	2,229
5. Delaware	0	1	2	3	5	8	0	19
Maryland	233	6	6	4	28	66	27	370
New Jersey	1	0	2	0	1	4	1	9
Sub-total	234	7	10	7	34	78	28	398
6. Georgia	1	0	2	0	4	0	1	8
North Carolina	0	0	13	8	11	8	4	44
South Carolina	0	0	4	2	1	1	1	9
Virginia	2	1	12	12	20	19	38	104
Sub-total	3	1	31	22	36	28	44	165
7. Florida	3	0	0	14	31	89	176	313
8. Michigan	133	16	35	42	36	49	31	342
9. Ohio	97	10	106	80	127	102	109	631
10. Kentucky	0	0	7	12	18	15	10	62
Tennessee	0	0	9	43	60	142	229	483
West Virginia	0	1	14	2	17	0	1	35
Sub-total	0	1	30	57	95	157	240	580
11. Alabama	0	0	1	5	1	79	1	87
Louisiana	0	0	0	1	0	1	0	2
Mississippi	0	0	0	0	9	18	41	68
Sub-total	0	0	1	6	10	98	42	157
12. Wisconsin	4	2	79	53	61	45	37	281
13. Illinois	28	20	164	95	96	70	1	474
Indiana	35	13	31	36	60	54	14	243
Sub-total	63	33	195	131	156	124	15	717
14. Iowa	7	28	101	71	44	32	58	341
Minnesota	0	0	31	10	28	21	11	101
Nebraska	0	0	3	2	1	2	0	8
South Dakota	0	0	4	1	0	0	0	5
Sub-total	7	28	139	84	73	55	69	455
15. Arkansas	0	0	1	0	0	5	0	6
Kansas	15	3	3	1	3	0	1	26
Missouri	0	0	3	13	19	35	19	89
Oklahoma	8	5	22	18	17	18	17	105
Texas	0	0	1	5	0	3	1	10
Sub-total	23	8	30	37	39	61	38	236
TOTAL	1,179	500	1,194	1,095	1,319	1,544	1,277	8,108



NORTH AMERICAN NEST RECORD CARD PROGRAM
YEAR
Shaded Boxes not to be completed by observer

Species: EASTERN BLUEBIRD
1 1 9 6 9

Observer (two initials, last name) In squares in space opposite → 15 M 17 B E L L

Locality (in relation to nearest town) 3 miles SE of Swanton

County LUCAS

State or Province OHIO

Elevation (in feet above sea level) 36 6 5 0

Fill in if known
Latitude 29 4 1 31 3 3
Longitude 41 0 8 3 44 5 2

HABITAT (circle where appropriate)
1. Woods 2. Swamp 3. Marsh 4. Field 5. Grassland 6. Desert 7. Tundra 8. Suburban 9. Urban
[✓ 0.] Other (specify) PARK
01. Coniferous [✓ 02.] Deciduous 03. Mixed 04. Orchard 05. Cultivated 06. Fallow 07. No Veget. 08. Hedgerow
09. Shrub 10. Salt 11. Brackish 12. Fresh 13. Sandy Beach 14. Gravel Beach 15. Other (specify)
DOMINANT PLANT(S) IN HABITAT (list one or two)
OAKS POPLARS

NEST SITE (circle where appropriate)
01 Bare ground 02 On ground in vegetation 03 Floating 04 Low vegetation 05 Shrub 06 Palm 07 Deciduous tree branch
08 Deciduous tree cavity 09 Conifer branch 10 Conifer cavity [✓ 11] Nest box 12 Other structure 13 Cliff or bank
14 Other (specify)
PRINCIPAL PLANT OR STRUCTURE SUPPORTING NEST STEEL PIPE

Height of Eggs Above Ground or Water in Feet (feet and tenths if under five feet) Feet Tenths 72 0 0 6 2

If parasited by Cowbird check here and see instructions. ☐
If same pair had other nestings this year, indicate which this is (1, 2, 3) (use separate card for each nesting) 77 1

PLEASE COMPLETE BOTH SIDES OF THE CARD

NORTH AMERICAN NEST RECORD CARD PROGRAM
YEAR
Shaded Boxes not to be completed by observer

Species: EASTERN BLUEBIRD
1 1 9 6 9 7 6 6 7 4 5 6

Observer (two initials, last name) In squares in space opposite → 15 M 17 B E L L

Locality (in relation to nearest town) 3 miles SE of Swanton

County LUCAS

State or Province OHIO 6 6

Elevation (in feet above sea level) 36 0 0 6 5 0

Fill in if known
Latitude 29 4 1 31 3 3 1
Longitude 41 0 8 3 44 5 2

HABITAT (circle where appropriate)
1. Woods 2. Swamp 3. Marsh 4. Field 5. Grassland 6. Desert 7. Tundra 8. Suburban 9. Urban
0. Other (specify) PARK
01. Coniferous [✓ 02] Deciduous 03. Mixed 04. Orchard 05. Cultivated 06. Fallow 07. No Veget. 08. Hedgerow 0
09. Shrub 10. Salt 11. Brackish 12. Fresh 13. Sandy Beach 14. Gravel Beach 15. Other (specify) 0 6
DOMINANT PLANT(S) IN HABITAT (list one or two)
OAKS POPLARS 2 1 0 0 0 5 2 0 7 0 0 1

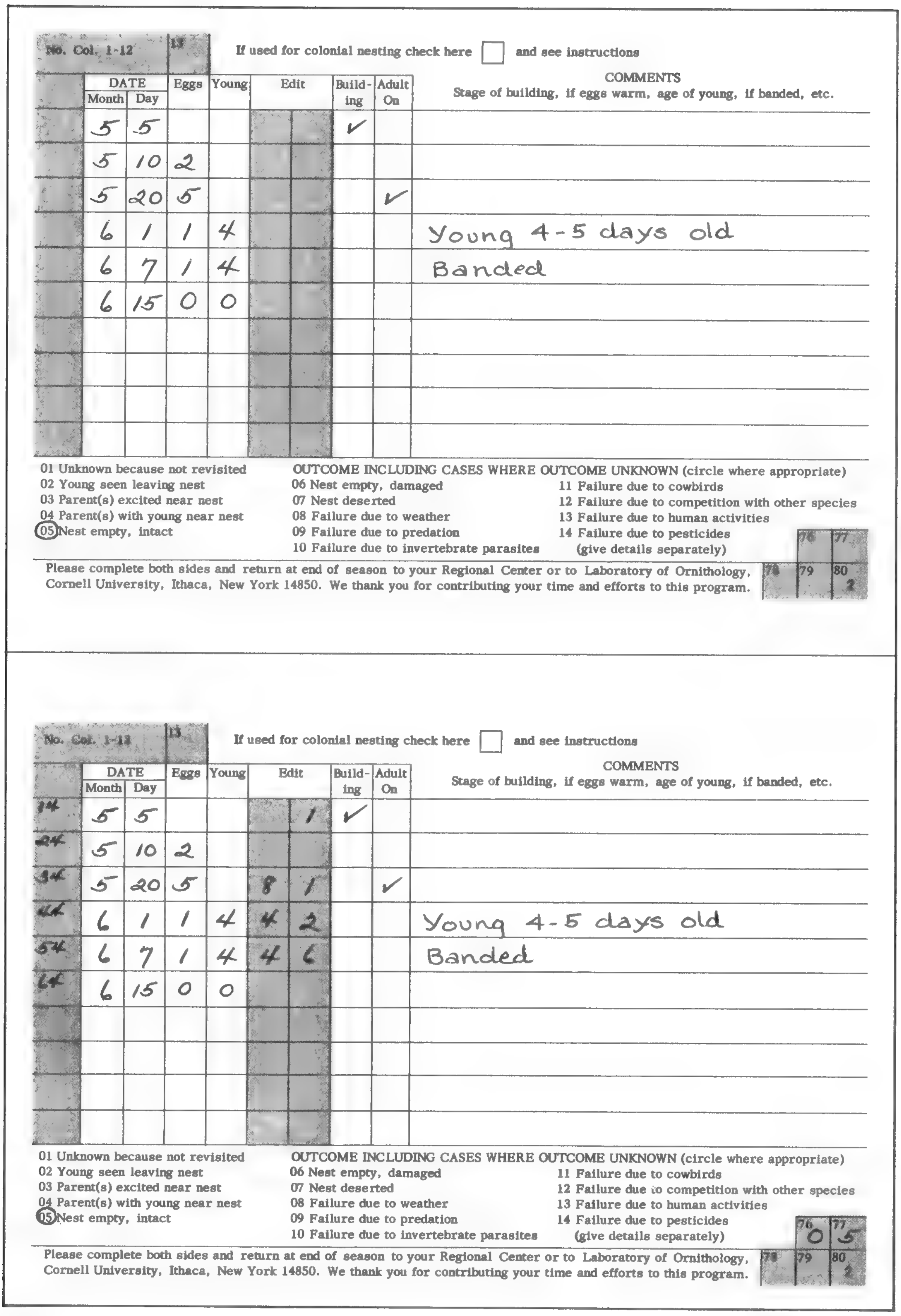
NEST SITE (circle where appropriate)
01 Bare ground 02 On ground in vegetation 03 Floating 04 Low vegetation 05 Shrub 06 Palm 07 Deciduous tree branch
08 Deciduous tree cavity 09 Conifer branch 10 Conifer cavity [✓ 11] Nest box 12 Other structure 13 Cliff or bank 1 1
14 Other (specify)
PRINCIPAL PLANT OR STRUCTURE SUPPORTING NEST STEEL PIPE

Height of Eggs Above Ground or Water in Feet (feet and tenths if under five feet) Feet Tenths 72 0 0 6 2

If parasited by Cowbird check here and see instructions. ☐
If same pair had other nestings this year, indicate which this is (1, 2, 3) (use separate card for each nesting) 77 1

PLEASE COMPLETE BOTH SIDES OF THE CARD

Figure 1. A nest-record card used in the program showing side one completed by an observer (*top*) and the same side after being edited at the Laboratory of Ornithology (*bottom*).



No. Col. 1-12 | 13 | If used for colonial nesting check here ☐ and see instructions

DATE Month	DATE Day	Eggs	Young	Edit	Edit	Build-ing	Adult On	COMMENTS Stage of building, if eggs warm, age of young, if banded, etc.
5	5					✓		
5	10	2						
5	20	5					✓	
6	1	1	4					Young 4-5 days old
6	7	1	4					Banded
6	15	0	0					

01 Unknown because not revisited
02 Young seen leaving nest
03 Parent(s) excited near nest
04 Parent(s) with young near nest
[✓ 05] Nest empty, intact

OUTCOME INCLUDING CASES WHERE OUTCOME UNKNOWN (circle where appropriate)
06 Nest empty, damaged
07 Nest deserted
08 Failure due to weather
09 Failure due to predation
10 Failure due to invertebrate parasites
11 Failure due to cowbirds
12 Failure due to competition with other species
13 Failure due to human activities
14 Failure due to pesticides
(give details separately)

76	77

78	79	80
		2

Please complete both sides and return at end of season to your Regional Center or to Laboratory of Ornithology, Cornell University, Ithaca, New York 14850. We thank you for contributing your time and efforts to this program.

No. Col. 1-12 | 13 | If used for colonial nesting check here ☐ and see instructions

	DATE Month	DATE Day	Eggs	Young	Edit	Edit	Build-ing	Adult On	COMMENTS Stage of building, if eggs warm, age of young, if banded, etc.
14	5	5				1	✓		
24	5	10	2						
34	5	20	5		8	1		✓	
44	6	1	1	4	4	2			Young 4-5 days old
54	6	7	1	4	4	6			Banded
64	6	15	0	0					

01 Unknown because not revisited
02 Young seen leaving nest
03 Parent(s) excited near nest
04 Parent(s) with young near nest
[✓ 05] Nest empty, intact

OUTCOME INCLUDING CASES WHERE OUTCOME UNKNOWN (circle where appropriate)
06 Nest empty, damaged
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11 Failure due to cowbirds
12 Failure due to competition with other species
13 Failure due to human activities
14 Failure due to pesticides
(give details separately)

76	77
0	5

78	79	80
		2

Please complete both sides and return at end of season to your Regional Center or to Laboratory of Ornithology, Cornell University, Ithaca, New York 14850. We thank you for contributing your time and efforts to this program.

Figure 2. A nest-record card used in the program showing side two completed by an observer (*top*) and the same side after being edited at the Laboratory of Ornithology (*bottom*).

we can never use this type of analysis as primary evidence of population change. He thought, however, it might draw attention to changes that would otherwise remain unnoticed and could subsequently be investigated by more reliable methods. I feel that the use of the nest-record cards for studies of population levels is probably limited to collecting data on breeding localities at the fringe of the range.

Biases of Data Recording

Several factors prejudice the data received from the field: geographical distribution of observers, their enthusiasm, variation of ease in finding nests, effect of observers on nests, and variation in methods employed by observers in looking for nests.

The geographical distribution of records from observers bears little relation to the actual distribution of the species, a fact clearly shown in the present analysis. Furthermore, the enthusiasm of the observer may wane as the season progresses and the nests become harder to find. These factors may bias the timing of breeding season as calculated from the nest-record cards.

I examined (Peakall, 1960) the effect of these biases by plotting the breeding season of the Yellowhammer (*Emberiza citrinella*) from the nest-record cards of the British Trust for Ornithology and comparing the results with data from an intensive field study on the species by Parkhurst and Lack (1946). The curve from the nest-record cards showed a higher and earlier peak than that in their study which they carried out for one entire breeding season. The peak of the breeding season in the two studies differed by five days, and a chi-square test on the data of the first and last halves of the season showed that the shift, though small, was significant at the one-per-cent level. However, an annual variation in nesting may have been partly responsible for the difference. The nest-record cards contained data for 20 years, 1939 to 1959; Parkhurst and Lack used data from a single season — 1944.

The data on clutch size appear to be less susceptible to bias. Using nest-record cards, Newton (1964) calculated 4.3 eggs for an average clutch of the Chaffinch (*Fringilla coelebs*), a figure that compares well to the clutch size of 4.4 from the unpublished diaries of Arthur Whitaker. For the Yellowhammer (Peakall, 1960), the nest-record cards indicated an average clutch of 3.5; Parkhurst and Lack (1946) found it to be 3.3 in their study.

The location of the nest biases the data in favor of the most conspicuous nests at lower levels. Working on the Long-tailed Tit (*Aegithalos caudatus*) in the field, Lack and Lack (1958) found only 62.5 per cent of the nests less than nine feet from the ground; their corresponding figure from the nest-record cards was 97 per cent. One might expect that biases of nest-site location would also affect the estimates of breeding success. Apparently, no one has yet investigated this point.

Nests, visited frequently by observers, produce another source of bias in that they may be more likely to fail. Mayer-Gross (1961) examined this problem for seven passerine species, dividing the nests into two groups: the first group was visited regularly; the second only once. He concluded that frequent inspections of a nest did not increase natural predation. However, this is a difficult problem to test experimentally.

A number of other factors may bias the data. Observers vary the number and timing of their visits; their reliability varies; and sometimes they record interpretations as facts. We find that many observers have considerable difficulty in recording the nature of the habitat. Many of these biases may lessen as the program advances and observers become more accustomed to recording their data.

In view of the innumerable biases, it is clear that a student making a breeding study of a particular species should not rely entirely on an analysis of the nest-record cards. The greatest value of the data from the cards lies in the added breadth and statistical strength of the information collected. No single observer could possibly obtain the records of more than 8,000 nests of the Eastern Bluebird, used in this study (see Table 1).

When we compare the data from one set of nest-record cards with the data from another, we assume that the biases remain constant, or, at least, tend to do so. Thus, by making an annual comparison of breeding parameters, it will be possible for us to monitor accurately the status of bird species.

Breeding Season

In the literature, the extreme dates of nesting usually determine the breeding season of a species. In this study, I have determined the breeding season by calculating the date on which the female completed the clutch and then totaling the number of such records for each 10-day period (see the Appendix for an explanation of the method). Table 2 shows the percentage of nests in which the clutches were completed within each 10-day period from 11 March to 27 August in the 15 areas. Table 3 gives the results year by year in Pennsylvania. The range in dates of the completed clutches for 90 per cent of the records appears in Table 2. I considered the 90-per-cent range a more meaningful expression of the breeding season than extreme dates, since very early and very late dates are likely to be due to abnormal behavior or weather conditions.

The breeding period for the Eastern Bluebird is shortest in the extreme north, in Canada and New England, Areas 1 and 2. This we expected. What we did not expect was that the breeding period is almost as short in the extreme southern part of the range, in Florida and the Gulf States, Areas 7 and 11. Surprisingly, the breeding period is shorter in Florida than in Illinois or Indiana. By comparing Figures 3 and 4, one can see that the longest breeding season coincides with the highest breeding density.

The Eastern Bluebird raises two broods throughout most of its range, shows a tendency for triple-broodedness in the central part, and single-broodedness in Canada (Figure 5). These conclusions correlate well with the findings of Musselman (1935) in Illinois, Laskey (1943) in Tennessee, and Thomas (1946) in Arkansas. Both Laskey and Thomas noted that bluebirds occasionally attempt a fourth nesting.

Clutch Size

The clutches of many species of European passerines increase in size from March to mid-June and decrease thereafter. Our data show that the clutch size

TABLE 2

Breeding Season of the Eastern Bluebird

Date interval	*Percentage of the clutches completed within each 10-day period for each area**														
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*
11 Mar. – 20 Mar.			0.16				0.67								0.88
21 Mar. – 30 Mar.			0.16		1.03	0.65	5.70		0.17	1.27			0.43		3.54
31 Mar. – 9 Apr.			0.08	0.89	1.54	3.92	11.07	0.61	0.33	5.61	5.30	0.37	2.30	0.46	10.18
10 Apr. – 19 Apr.		3.13	2.27	8.27	12.56	11.76	22.48	1.22	9.52	21.70	28.48	0.75	8.05	2.30	14.16
20 Apr. – 29 Apr.	5.37	10.16	11.93	12.27	12.05	17.65	7.72	13.72	18.03	6.87	16.56	2.99	16.52	14.02	9.73
30 Apr. – 9 May	11.41	15.63	15.50	14.01	13.85	7.19	3.36	14.94	10.52	3.44	1.32	8.96	10.49	14.25	7.52
10 May – 19 May	10.74	9.38	11.61	8.65	8.46	5.23	6.38	8.84	7.35	5.79	1.32	10.07	8.33	7.36	7.52
20 May – 29 May	11.41	13.28	11.04	8.84	7.69	6.54	12.42	11.28	7.68	8.32	3.97	23.88	7.33	13.33	9.29
30 May – 8 June	13.42	10.94	9.82	9.50	7.44	9.15	13.42	14.33	11.52	9.40	13.25	14.18	8.33	10.11	10.18
9 June – 18 June	19.46	12.50	12.66	12.32	9.23	14.38	9.73	12.20	12.02	10.31	11.92	9.70	13.51	16.09	9.29
19 June – 28 June	9.40	8.59	11.04	11.94	10.51	5.23	4.70	12.50	10.18	7.23	9.27	13.43	7.76	10.57	6.19
29 June – 8 July	6.04	6.25	6.57	7.52	4.62	7.19	2.35	4.88	6.18	5.79	2.65	7.09	5.17	6.44	7.08
9 July – 18 July	8.72	5.47	4.63	3.67	7.18	7.19		3.96	3.34	7.41	3.31	5.60	5.60	2.53	2.21
19 July – 28 July	4.03	4.69	1.62	1.83	2.56	1.96		1.22	2.34	4.34	2.65	1.49	3.02	1.61	1.77
29 July – 7 Aug.			0.81	0.19	0.77	1.96		0.30	0.33	1.63		1.12	1.87	0.46	0.44
8 Aug. – 17 Aug.			0.08	0.05	0.26					0.90		0.37	1.15	0.46	
18 Aug. – 27 Aug.				0.05									0.14		

*See Table 1 for locality of each numbered area.

TABLE 3

Annual Variation of Breeding Season, Clutch Size, and Breeding Success of the Eastern Bluebird in Pennsylvania

Date interval	*The breeding season expressed as percentages of completed clutches for 10-day intervals*							
	Prior to 1964	*1964*	*1965*	*1966*	*1967*	*1968*	*1969*	*Total*
31 Mar. — 9 Apr.		0.63	1.57	1.21	1.38	1.42	0.29	0.89
10 Apr. — 19 Apr.	0.25	12.58	2.62	6.88	12.43	19.34	7.45	8.27
20 Apr. — 29 Apr.	8.61	25.79	4.19	12.15	11.05	13.68	20.34	12.27
30 Apr. — 9 May	23.80	14.47	22.51	10.53	5.80	8.96	10.03	14.01
10 May — 19 May	8.10	7.55	17.28	8.50	8.01	3.77	8.60	8.65
20 May — 29 May	8.35	3.14	8.38	12.55	12.43	6.13	7.16	8.84
30 May — 8 June	9.87	14.47	4.71	11.34	10.50	11.08	10.32	9.50
9 June — 18 June	11.39	8.81	9.42	12.15	11.33	16.51	10.03	12.32
19 June — 28 June	15.70	8.81	7.85	12.96	13.54	10.14	11.17	11.94
29 June — 8 July	9.11	3.14	16.23	6.07	7.46	4.01	5.73	7.52
9 July — 18 July	2.78	0.63	4.71	4.05	3.87	2.12	5.73	3.67
19 July — 28 July	2.03	0.00	0.52	1.62	1.93	2.83	1.72	1.83
29 July — 7 Aug.					0.28		0.86	0.19
8 Aug. — 17 Aug.							0.29	0.05
18 Aug. — 27 Aug.							0.29	0.05
Number of	395	159	191	247	362	424	349	2,127
	Clutch size (mean, standard deviation, and sample size)							
	4.59 ± 0.75 (279)	4.62 ± 0.69 (132)	4.61 ± 0.73 (151)	4.55 ± 0.85 (172)	4.53 ± 0.83 (224)	4.61 ± 0.78 (253)	4.49 ± 0.75 (189)	4.57 ± 0.77 (1,400)
	Overall breeding success							
	74.8%	79.0%	73.3%	79.8%	66.1%	64.4%	73.6%	72.1%

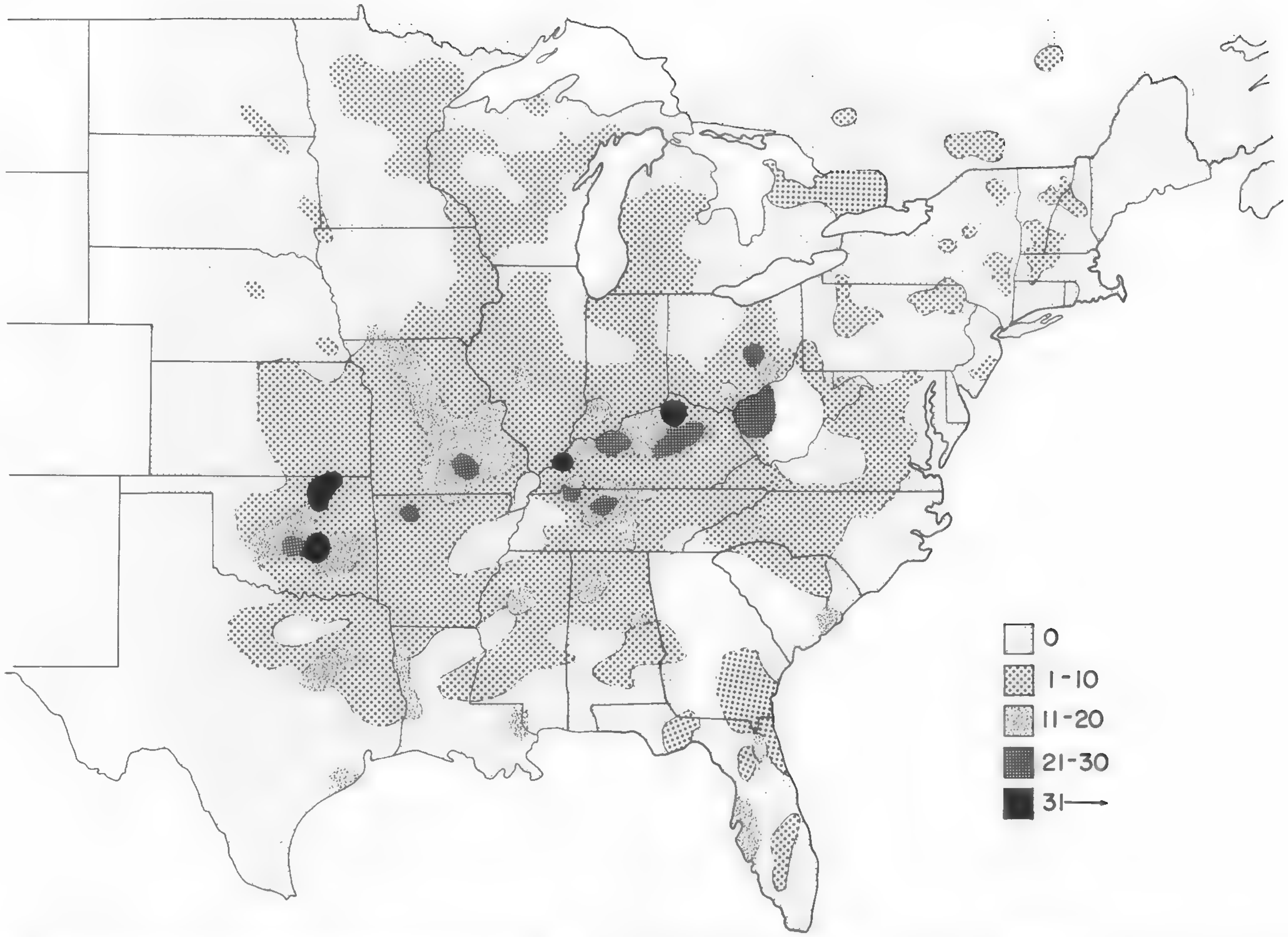

Figure 3. The relative density of the Eastern Bluebird throughout its breeding range in 1968. Map prepared by the author from the data of the breeding bird survey of the U.S. Fish and Wildlife Service, courtesy of Chandler S. Robbins. The values shown on the map indicate the number of bluebirds seen or heard every half-mile along a prearranged 25-mile route. Each stop lasted three minutes.

TABLE 4

Seasonal Variation in Clutch Size of the Eastern Bluebird for Fifteen Areas*

Details for Pennsylvania (Area 4) for each 10-day period

Date	*Clutch size*	*Maximum eggs*
31 Mar. – 9 Apr.	5.11 ± 0.60(9)	4.88 ± 0.70(17)
10 Apr. – 19 Apr.	5.16 ± 0.74(83)	4.89 ± 0.90(175)
20 Apr. – 29 Apr.	4.82 ± 0.78(163)	4.72 ± 0.83(260)
30 Apr. – 9 May	4.74 ± 0.71(219)	4.62 ± 0.90(297)
10 May – 19 May	4.74 ± 0.78(148)	4.64 ± 0.86(183)
20 May – 29 May	4.75 ± 0.65(135)	4.67 ± 0.84(188)
30 May – 8 June	4.61 ± 0.64(119)	4.49 ± 0.87(202)
9 June – 18 June	4.47 ± 0.72(146)	4.28 ± 0.85(261)
19 June – 28 June	4.25 ± 0.75(181)	4.19 ± 0.79(254)
29 June – 8 July	4.11 ± 0.58(112)	3.98 ± 0.76(158)
9 July – 18 July	3.94 ± 0.60(54)	3.82 ± 0.70(78)
19 July – 28 July	3.75 ± 0.59(28)	3.72 ± 0.65(39)
29 July – 7 Aug.	3.50 ± 0.71(2)	3.50 ± 0.58(4)
8 Aug. – 17 Aug.		3.00 ± 0.00(1)
18 Aug. – 27 Aug.	3.00 ± 0.00(1)	3.00 ± 0.00(1)
Overall average	4.57 ± 0.77(1400)	4.46 ± 0.89(2118)

Summary of clutch size variation for all areas

Area number	*Location*	*Overall average*
1	Quebec, Ontario	4.18 ± 0.79(51)
2	New England	4.34 ± 0.92(68)
3	New York	4.58 ± 0.80(826)
4	Pennsylvania	4.57 ± 0.77(1400)
5	Delaware, Maryland, New Jersey	4.35 ± 0.77(139)
6	Georgia, Carolinas, Virginia	4.40 ± 0.79(86)
7	Florida	4.33 ± 0.78(227)
8	Michigan	4.52 ± 0.76(156)
9	Ohio	4.55 ± 0.77(350)
10	Kentucky, Tennessee, West Virginia	4.48 ± 0.75(346)
11	Alabama, Louisiana, Mississippi	4.36 ± 0.76(118)
12	Wisconsin	4.51 ± 0.79(112)
13	Illinois, Indiana	4.52 ± 0.78(292)
14	Iowa, Minnesota, Nebraska, South Dakota	4.54 ± 0.80(276)
15	Arkansas, Kansas, Missouri, Oklahoma, Texas	4.52 ± 0.92 (151)

*Numbers include the average, standard deviation, and sample size (in parentheses).

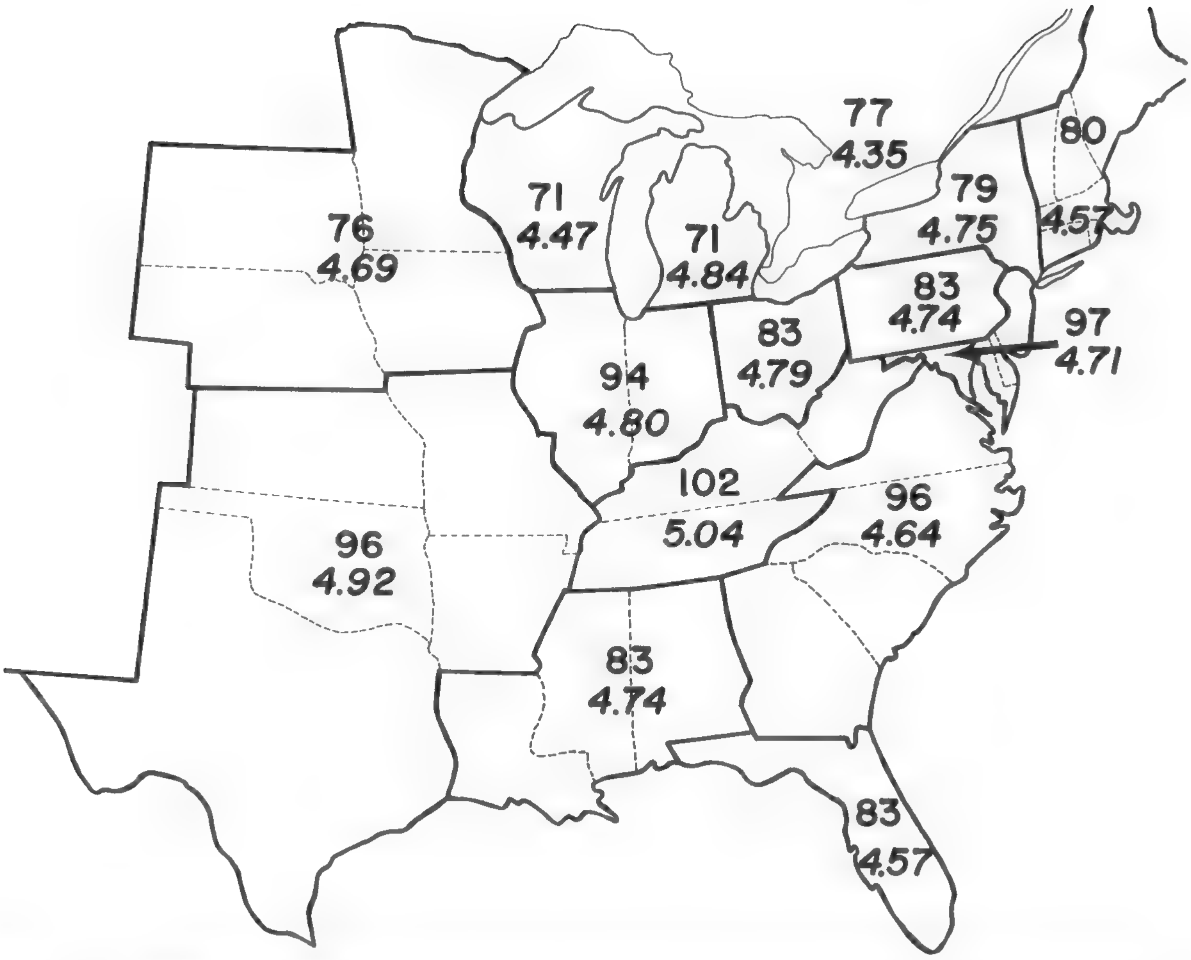

Figure 4. Geographical variation of the duration of the breeding season and of the clutch size at the peak of the breeding season. The values for each of the 15 areas are given in days (*above*) and the number of eggs per clutch (*below*). The clutch size is greatest in areas of greatest breeding density and where the breeding season is the longest.

of the bluebird, in some areas, is slightly smaller for the first 10 days of the breeding season, but the trend is not pronounced. On the other hand, the decrease in the size of the clutch toward the end of the breeding season shows up well for the bluebird in all 15 areas (see Table 4 for Pennsylvania). Laskey (1940) recorded the same phenomenon, and calculations from Thomas' data (1946) show it also. We examined the data from Pennsylvania for an annual variation in clutch size and found it to be slight (Table 3).

The computer calculated the variation in clutch size for the 15 Areas throughout the breeding season (Table 4) and at the peak of the breeding season (Figure 4). We did not find an increase in clutch size with an increase in latitude as noted for many species in the Old World (Lack, 1947), including the European Robin, *Erithacus rubecula* (Lack, 1943). In the bluebird, the maximum clutch size occurs at the center of its range and decreases toward the periphery both north and south. This area of higher clutch size also coincides, as did the longer breeding season, with the area of highest population density (Figure 5).

I used data for clutch size only when I knew the clutch was complete. In the case of abnormally small clutches, the adult's presence on the nest indicated the existence of a complete and active clutch. A calculation of the clutch size on the basis of maximum number of eggs present — even though the observer visited the nest only once – lowered the average clutch size, but not significantly. This is reasonable when one considers that a number of nests with only one or two eggs must have been included in the figures.

Breeding Success

The ultimate success of a species depends upon the net productivity. The computer calculated the breeding success in two parts: First, the percentage of nests that were at least partially successful (a nest was considered a success even if only one young fledged); second, the individual losses from nests that were partially successful.

The percentage of nests at least partially successful varied from a low of 52.1 per cent in Area 14 (Iowa, Minnesota, South Dakota, and Nebraska) to 78.3 per cent in Area 5 (Delaware, New Jersey, and Maryland). In all but two of these Areas, 13 and 15, our figures showed more failures in nests with young than in nests with eggs. Ricklefs (1969), summarizing the data from many field studies, came to the opposite conclusion although our figures for overall breeding success agree well with his. The difference may have resulted from the fact that I determined nest failures by averaging the last date that I knew the nest was active with the first date that I knew it had failed. My procedure may have indicated too large a number of failures of nests where there were young, especially if there was a long interval between dates. However, the overall breeding success would not be affected. I divided the individual losses into four categories: infertile eggs, loss of eggs for other reasons, loss of young, and losses not assigned to either the egg or young.

It is rare for single eggs to disappear from an otherwise successful clutch. No more than 3.6 per cent of the eggs disappeared without the clutch, of which they were a part, also disappearing. On the other hand, the percentage of infertile eggs showed a considerably higher variation, ranging from lows of 2.6 and 3.0 per cent in the extreme east and west, Areas 5 and 15, to a high of 12.1 per cent in Florida, Area 7. Most of the losses, due to infertility, showed regional percentages of less than 7.0 per cent. Thomas (1946) found infertility as high as 8.8 per cent in bluebird nests. And Laskey (1939) and Musselman (1935) recorded comparable losses of 8.0 and 8.6 per cent, respectively. Musselman found considerable annual variation in the percentage of infertile eggs: 5.1 per cent in 1933, 13.4 per cent in 1934, 7.0 per cent in 1935. He also noted a substantial increase in the percentage of infertile eggs in second nestings: from 1.0 to 11.0 per cent in 1933, 7.0 to 23.1 per cent in 1934, and 5.0 to 9.9 per cent in 1935. The seasonal variation found by Laskey (1939) was less marked, 7.6 per cent for the first period, 4.3 per cent for the second, and 10.0 per cent for the last. In analyzing our data on infertile eggs by monthly periods, I found no clearcut pattern.

The Eastern Bluebird experienced the highest overall individual mortality in Florida (31.7 per cent), Wisconsin (23.4 per cent), and Michigan (23.0 per cent) and the lowest in the Gulf States (11.6 per cent), Arkansas, Kansas, Oklahoma, and Missouri (13.2 per cent), and Ontario and Quebec (13.9 per cent). No clinal pattern emerged from this analysis.

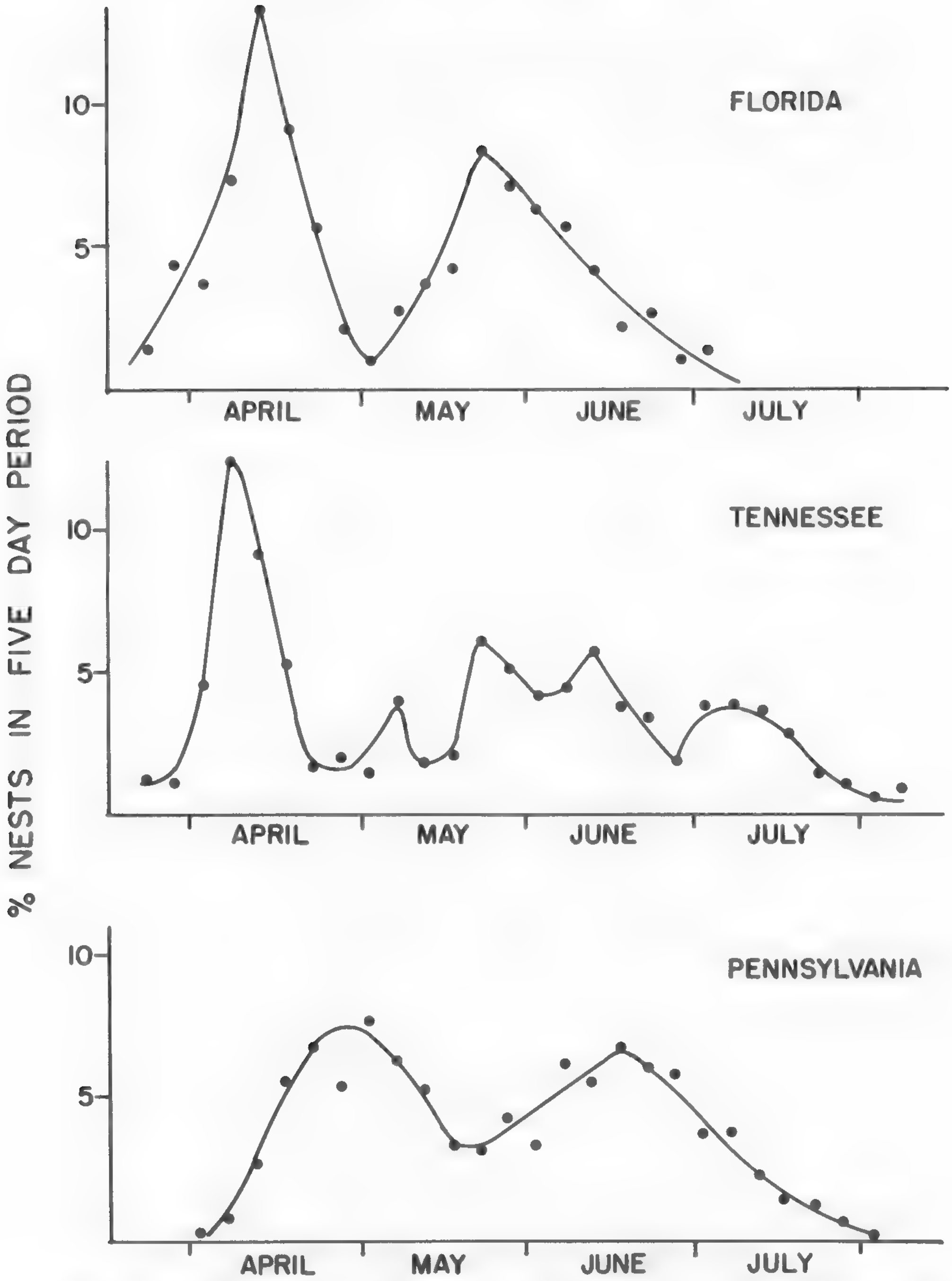

Figure 5. These graphs show the peak of the breeding season. The percentage of nests found are measured against time (five-day periods) and calculated by the computer from the nest record card data. The three areas under consideration show a distinct tendency toward double broods. Peak nesting in all areas occurs in April.

Comparison of Central and Peripheral Range Data

The data, analyzed from the nest-record cards, indicate that the Eastern Bluebird experiences a longer breeding season in areas of highest summer population density, with somewhat shorter seasons both to the north and south. Similarly, bluebirds tend to lay slightly larger clutches in areas of high density, again the middle portion of the range. These findings vary from those of Lack (1947), who showed that, for many passerines in the Old World, the clutch size tends to increase northward. This phenomenon should be checked in other species. With the increase of interest in nest-record card programs in Europe, outside of the British Isles, better statistical information should be available soon. We need additional field work to explain the differences between the central and peripheral portions of the range.

The Future of the North American Nest-record Card Program

The North American Nest-record Card Program serves as a center for the collection, analysis, and distribution of data on the breeding biology of birds. To accomplish its objective, the data must be available for research by others. The computerization of the program, now in progress, will increase the availability of the data. Without a data-retrieval system, the only source of information is in the original cards. Understandably, we are reluctant, as are most programs, to lend these irreplaceable source documents.

One of our major objectives is to use the North American Nest-record Card Program as an environmental monitor of the status of bird populations on the continent. A basic concept underlying this function holds that environmental pollution, especially by pesticides, reduces avian breeding success (Peakall, 1970). Since the program will accumulate great numbers of cards for many species, the statistical significance of even small changes will show up. We can examine readily such problems as the effects of DDT spraying for Dutch-elm disease and treatment for gypsy-moth control. Besides providing a monitoring system for the effect of pesticides, the Nest-record Card Program will give us a basis for studying changes caused by drought, land-usage, and habitat deterioration.

Summary

As an introduction to this paper, the first major analysis of a single species in North America, based on nest-record cards, I have outlined briefly the history of nest-record card programs and have discussed several factors that may bias the records received from the field.

In this study, 8,108 nest-record cards of the Eastern Bluebird (*Sialia sialis*) were analyzed by a computer to determine the timing of the breeding season, the clutch size, and the breeding success. The breeding season was longest in the middle latitudes of the species' range where the breeding density is highest. Bluebirds tended to lay slightly larger clutches in the center of their range at the height of the breeding season. The clutch size decreased as the breeding season progressed in all areas. I noted no geographical pattern of breeding success.

Acknowledgments

This article was made possible by the contributions of several hundred field observers. I wish I might acknowledge all of them individually, but that is impossible. The contribution of Mr. Ralph Bell of the Brooks Bird Club and Mr. William Highhouse deserve special mention. In addition to our own data, we borrowed substantial numbers of cards from the Maryland and Ontario Nest-record Card Schemes.

Mrs. Edith Edgerton, our Administrative Assistant, handled most of the correspondence and many other clerical matters related to our program. Mr. James W. Grier, Mrs. Taylor Lewis, Mrs. Teresa Osbourne, and Mrs. Robert J. Pantle edited the cards and developed the necessary computer programs. Mr. Robert J. Pantle and Mr. Chandler S. Robbins have given us invaluable advice throughout the program.

The generous support of Mrs. Bradley Fisk over the last three years enabled us to initiate the computerization of the Nest-record Card Program and was critical to the success of the enterprise. We also received support from the National Science Foundation (Grant GN-859).

APPENDIX

Editing and Analyzing Nest-record Cards

Figure 1 shows diagrammatically the overall editing process. After glancing at the nest-record card to make sure that it contains reasonable and useful ornithological data, the editor completes the shaded boxes. The contents of the boxes are then punched onto IBM cards, one IBM card being used for each side of the original nest-record card. The accuracy of the original data, the editing, and the punching process are checked by a pre-edit computer program during the stage of feeding the data into the computer.

A detailed account of the computer program used for the analysis of nest-record cards cannot be given here. Still, I shall outline the methods employed so that the reader can consider how I arrived at the conclusions in this article.

First the computer reconstructs as accurately as possible the most probable course of events. The accuracy, with which the computer performs this task, depends at what stage of the breeding cycle the nest was found (nest stage) and the number of subsequent visits by the observer. The calculated record will be more accurate if the observer makes a number of visits to each nest rather than one visit, and if the observations cover most of the nesting cycle.

The computer first determines the stage of the nesting cycle at the time of the first visit: (1) building, (2) incomplete clutch, (3) completed clutch, (4) eggs only, no further information available, (5) eggs and young, (6) young, (7) active, but contents unknown, or (8) deserted.

The next step calculates the most probable date of completion of the clutch. Certain criteria —listed below—must be correlated with the existing data. If the first criterion does not fit the data, the second criterion is examined, and so on. In each case the maximum error of the calculation is determined.

Criterion 1. If successive visits to the nest showed an increase in the number of eggs, then the computer assumed the laying of one egg each day and calculated the date of completion of the clutch accordingly.

Criterion 2. If the observer found a nest with both eggs and young, and at least one of the eggs subsequently hatched, then the computer subtracted the length of the incubation period (12 days for the Eastern Bluebird, Bent, 1949) from the first date shown on the card.

Criterion 3. If the nest-record card contained only a single date showing egg contents, with no further data indicating the subsequent number of young, then the computer subtracted one-half of the incubation period (6 days) from the date shown on the card to arrive at the date of completion of the clutch.

Criterion 4. If the observer recorded several dates showing that the nest contained eggs but no young, then the computer determined the completion of the clutch by subtracting one-half the incubation period (6 days) from the average of the dates shown on the card.

Criterion 5. If the observer recorded several dates showing both eggs and young (but not on same visit), then the computer first calculated the most probable date of hatching by averaging the dates of eggs and young shown on the card. From this date it then subtracted the length of the incubation period to arrive at the date for completion of the clutch.

Criterion 6. If the observer recorded dates showing the age of the young, then these data, plus the incubation period, was subtracted to give the completion date of the clutch. If the observer provided no information on age of the nestlings, then the average date of those given on the card was calculated. From this date the computer subtracted the incubation period (12 days) plus one-half the fledging period (16 days, Bent, 1949).

To determine the clutch size, the data on the card must conform to one of the following criteria:

Criterion 1. If two visits made on different days showed no change in the number of eggs, then this number was taken as the clutch size. If the observer recorded an abnormally small clutch, the computer used these data only if the nest-record card provided evidence that the nest had not been deserted.

Criterion 2. A sufficient interval of time must have occurred between two visits so that an incomplete clutch, recorded on the first visit, becomes a completed clutch on the subsequent visit (assuming a normal daily rate of laying).

Criterion 3. If the observer makes a single visit to a nest with eggs, the number of eggs recorded can be used as the clutch size only when the observer, on a subsequent visit within the normal incubation period, records the number of young in the nest.

I calculated the breeding success by using essentially the same method described by Mayfield (1961). Basically, the mortality rates are expressed in terms of nest days, and the calculations initially consider the nest as a whole rather than individual eggs or young. The number of nests, known to fail during the incubation period, was divided by the number of the nest days that eggs were present. The same procedure was used for calculating mortality during the fledging period. The losses of individuals from otherwise successful nests (nests from which at least one young fledged) were calculated in four categories: (1) loss of eggs, (2) number of eggs that failed to hatch, (3) loss of young, and (4) losses which could not be definitely assigned to either egg or young stages. These individual losses were used to correct the overall breeding success calculated on a whole-nest basis.

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Eastern Bluebird, *Sialia sialis*. Painting by J. H. Czech.

A PHOTOGRAPHIC STUDY OF THE POTOO IN COLOMBIA

José Ignacio Borrero H.

Photographs by the author

Little has been published about the Common Potoo. The following paper by Alexander F. Skutch is the most thorough study yet reported on this bird. Still, many questions remain unanswered.

On 13 January 1969, I began to study a pair of Crimson-crested Woodpeckers (*Phloeoceastes melanoleucus*) that nested in an old *Cecropia* tree at the edge of the Cauca River near Cali, Colombia. One of them flew to another *Cecropia* tree some 200 meters away. As I focused my telescope to locate the woodpecker, I encountered a Common Potoo (*Nyctibius griseus*) perched on a truncated branch some 15 meters from the ground. It sat erect with its bill in a horizontal position. I approached to observe it better. As I arrived within 25 meters of the tree where it was sitting, the potoo raised its head slowly, its bill assuming a nearly vertical position. It closed its eyes so that only dark slits marked their position. It remained stationary.

The Common Potoo requires an upright, broken branch of certain thickness on which to roost and nest, and also one that has a slight depression in the end of sufficient depth to support an egg.

The adult blends well with its surroundings, as can be seen easily in the photographs—so much so that I frequently had difficulty pinpointing the bird the following day, although I knew where its nest was. The bird's behavior greatly enhances the crypticity of the plumage.

I continued to visit the site and observe the potoo as often as other commitments permitted—usually two or three times each week. Whenever I did, I tried to photograph it. On 25 January, I found a second potoo sitting, like the other, at the end of a truncated branch and at about eight meters above the ground. Approximately 500 meters of mostly open country separated the trees in which the two potoos roosted.

By 11 February, it was apparent that both potoos were sitting with nestlings. I do not know when these young hatched. Both were small and inconspicuous, being almost completely covered by the parent most of the time. When they were exposed, they did not raise the bill at this early age although the parent always did so whenever I was in the vicinity.

The nests of both birds were in the end of a broken vertical branch less than eight inches in diameter and with a shallow depression less than one inch deep.

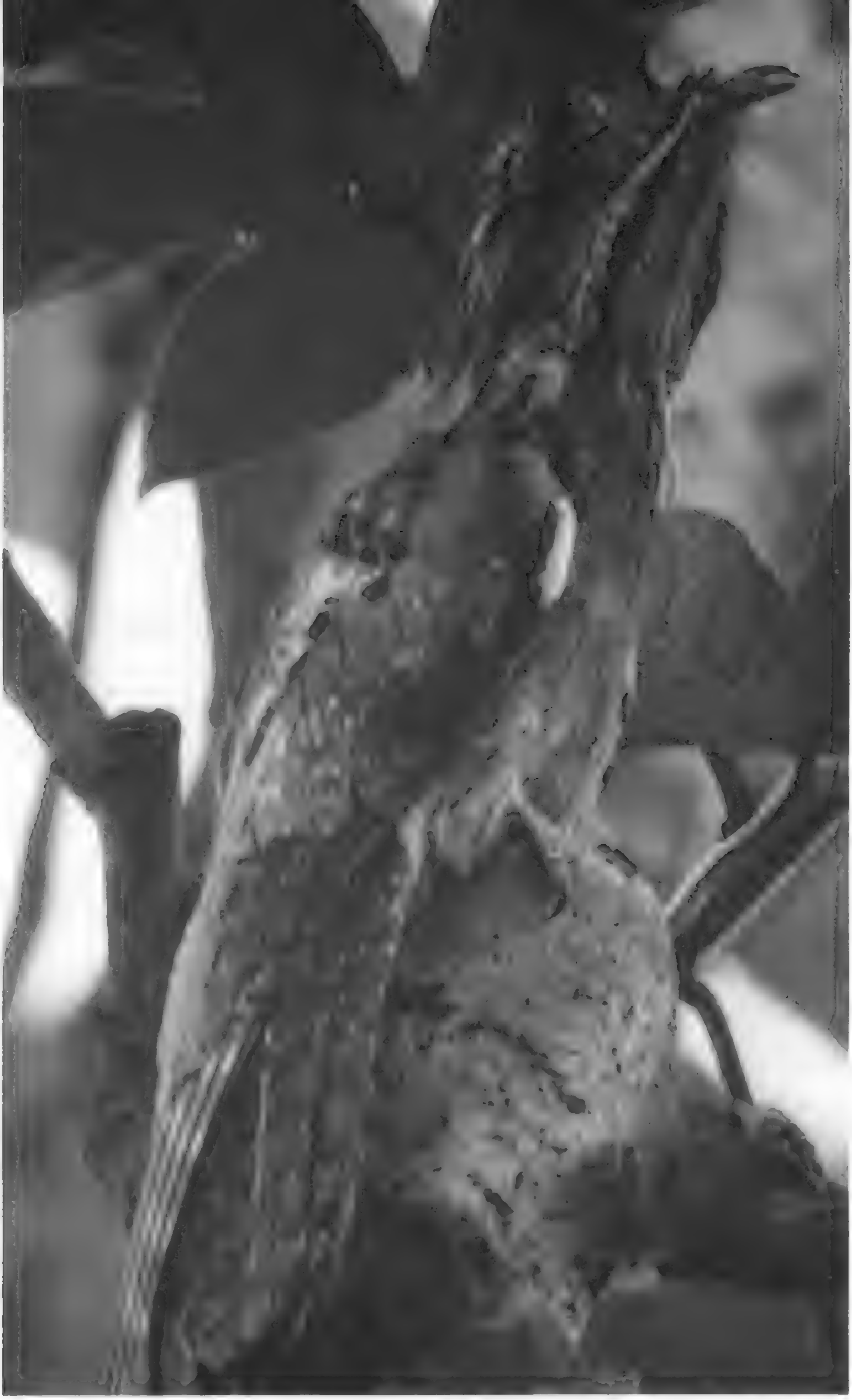

Figure 1. A Common Potoo sits in a cryptic posture, its mottled plumage simulating the bark of the tree.

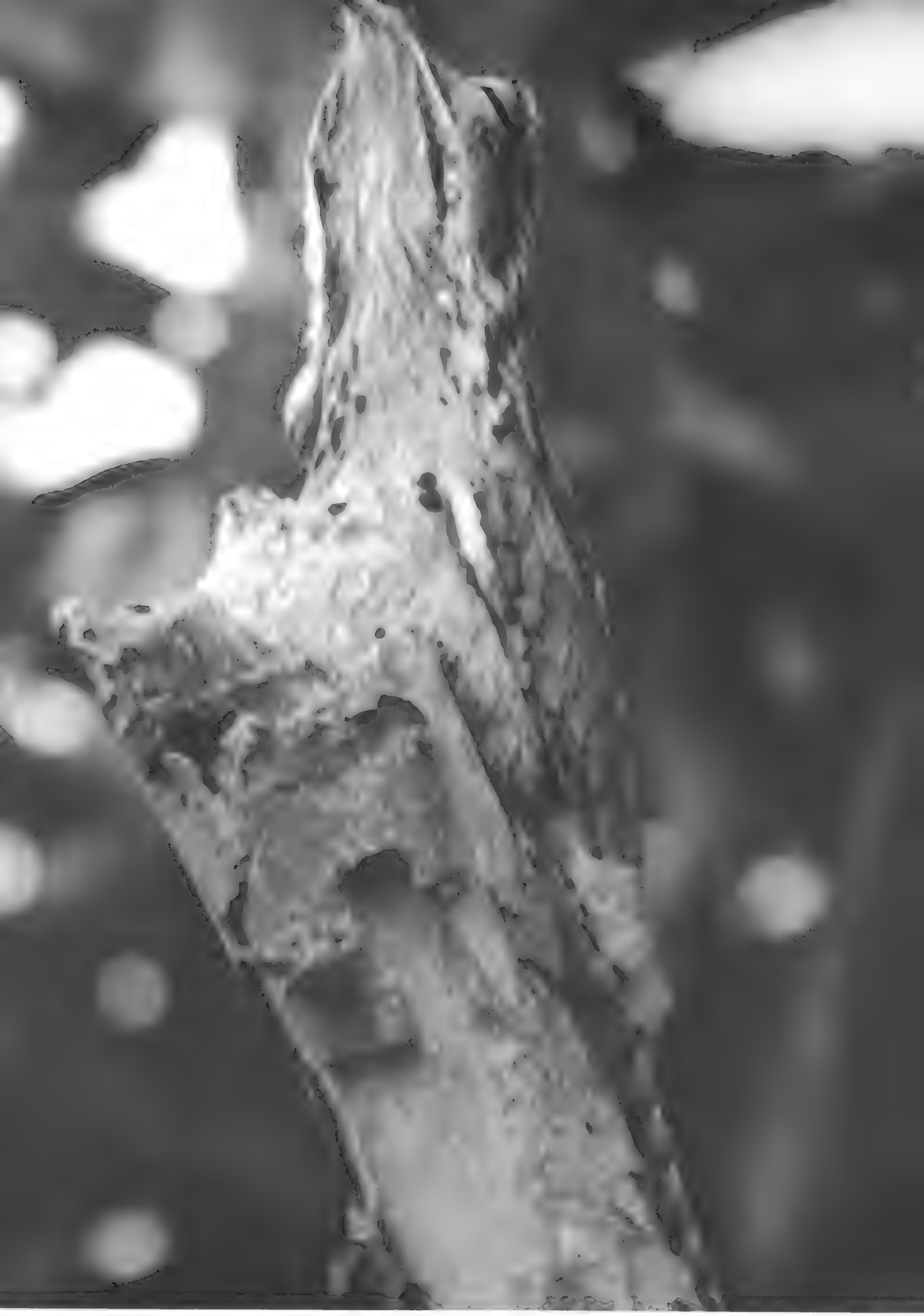

Figure 2. Another potoo appears to be an extension of the branch on which it rests. A single chick can be seen sitting in front of the adult.

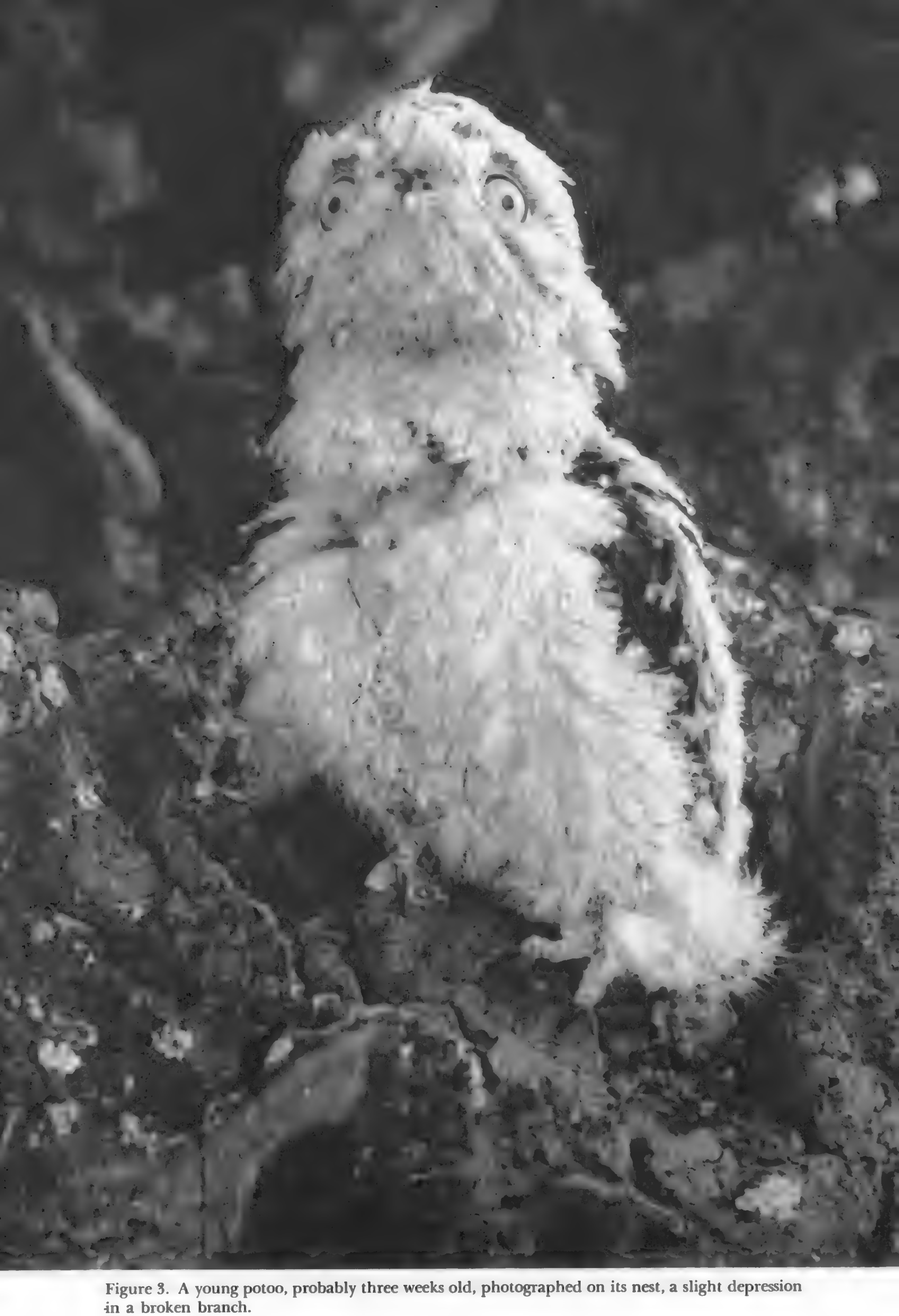

Figure 3. A young potoo, probably three weeks old, photographed on its nest, a slight depression in a broken branch.

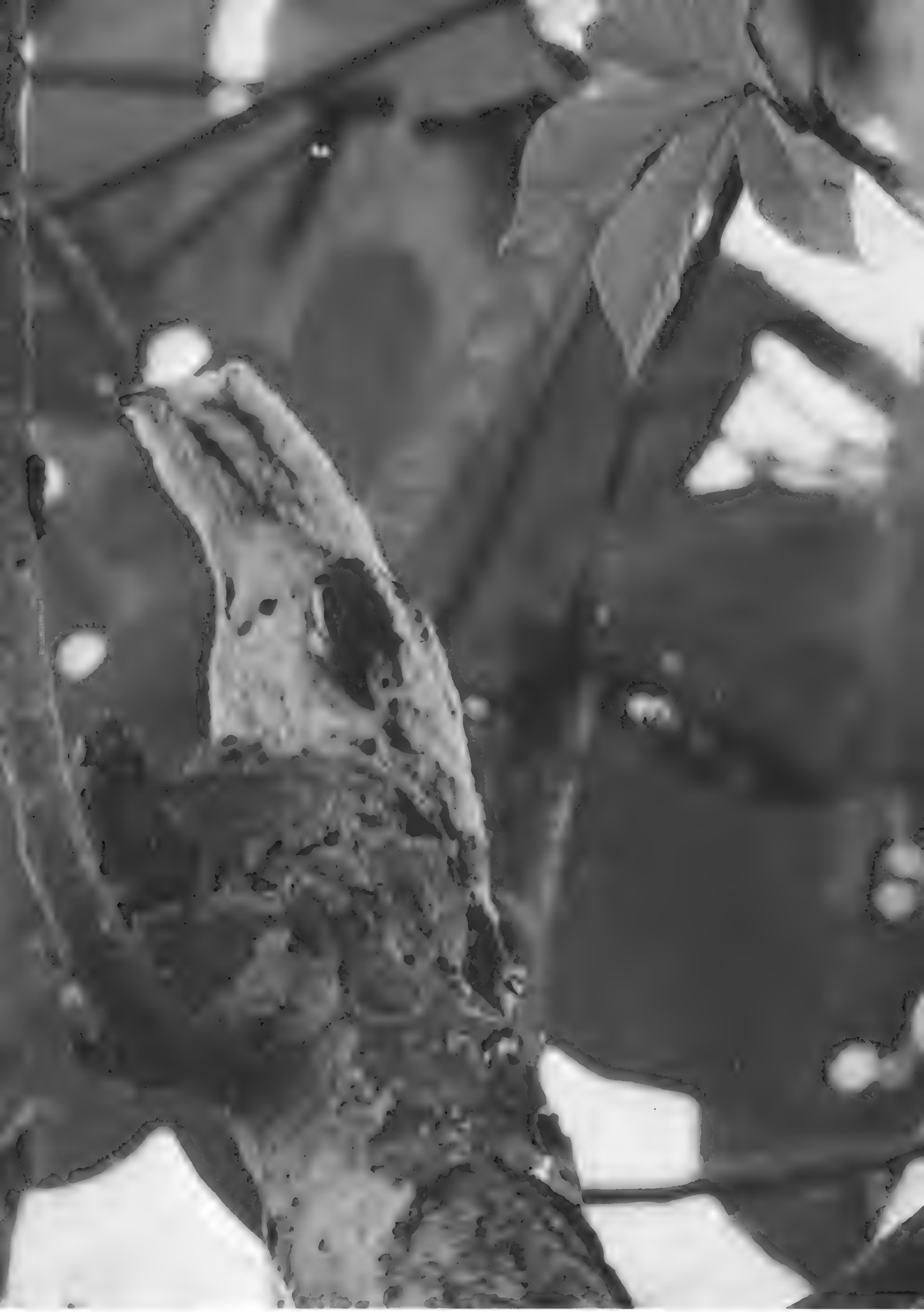

Figure 4. This young potoo, now about five weeks old, sits on its nest in the cryptic posture typical for its species.

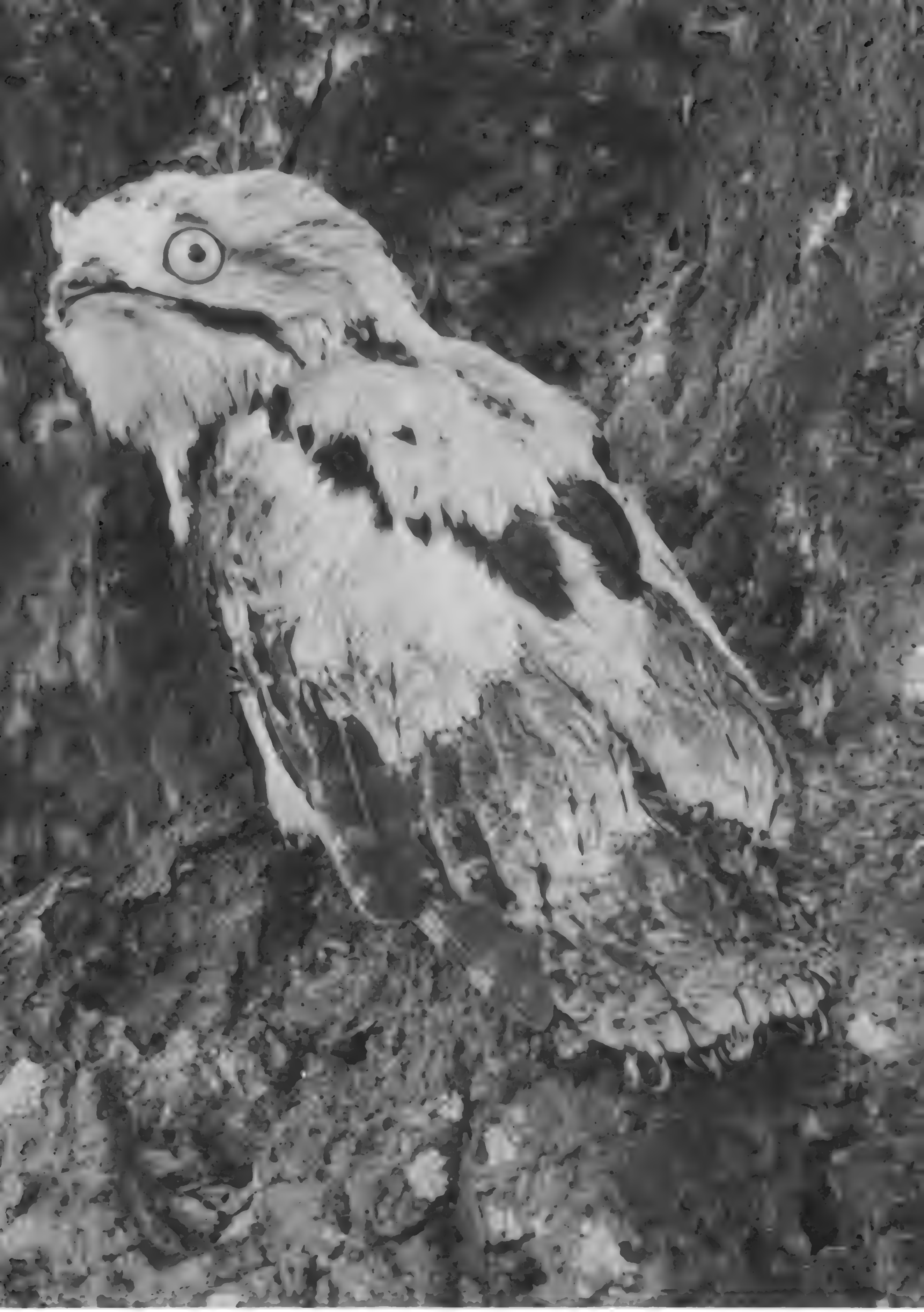

Figure 5. At about six to seven weeks of age, this bird flew from the nest when I climbed the tree to photograph it.

On 13 February, I noted the accelerated development of the young birds, but still they were inconspicuous, especially when seen from the ground.

By 15 February, the nestlings had grown so large that I could see them with ease when they stood at the edge of the nest in front of, or at the side of, the parent. The nestlings wore a conspicuous cream-colored plumage that had a pale pinkish tint. I noted that now the young potoos in both nests also raised the bill and remained stationary when they were conscious of my presence.

On 1 March, I decided to watch for the parents arriving to feed the nestlings, to find out, if possible, at what hour they did so. Placing an observer at one nest, I hid some 15 meters from the other nest. At 18:55 hours, at the nest I was watching, an adult flew into the nest tree, passing in front of me at a height of only about three meters. It was already dusk. At 19:03 an adult arrived and landed at the nest beside the young bird. I could see the two silhouettes perfectly, but it was too dark to observe any details or activity. The observer at the other nest had seen a large bird, possibly one of the parents, leave a neighboring tree.

With the hope of photographing a nestling at close range, I attempted to capture one on 11 March. My activity in climbing the tree caused it to fly, possibly for the first time. It landed at a site about one hundred meters away. When I found this nestling, it was alert and stationary with the bill in a horizontal position. As I tried to capture it, it flew again, this time another 50 meters and obviously with greater difficulty. I located it this time, sitting on a low branch of a shrub where I finally caught and photographed it. When I replaced the nestling gently in its nest, it remained quiet, showing no intention of flying and allowing me to approach no less than 20 inches with my camera. Although at this distance it did not attempt to camouflage itself by characteristically raising its bill, it did show intention to attack or strike by opening its enormous mouth and facing me.

During the day the nestlings panted and gular-fluttered forcefully with bill partially opened and directed upward. The tropical sun, from which they had practically no protection, shone directly on them at times.

By 19 March, the parents had abandoned their respective nests and were possibly roosting nearby, but not in the nest trees and no amount of searching in the neighboring trees revealed their whereabouts.

On that day I brought one of the nestlings down from the tree and photographed it. Then I returned it to its nest. By now, 19 March, the tarsi were grayish, the bill black with a white tip, and the eyes large and yellow with greatly reduced pupils. The general plumage coloration was cream with a pale pinkish hue, with the pink more pronounced on the forehead. Above and below the fine dark spots, characteristic of the adult, stood out. And already I perceived the well, but not yet fully, developed remiges and rectrices.

On 17 March, I noted that for the first time one of the nestlings was sitting outside its nest—about five meters away—on another branch in the same tree. By 20 March, the other nestling had abandoned its nest completely. Two days later both the young and the adults disappeared. I have not seen any potoos since in the vicinity.

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Tony Angell

Swainson's Hawk, *Buteo swainsoni*. Drawing by Tony Angell.

LIFE HISTORY OF THE COMMON POTOO

Alexander F. Skutch

The potoos are a small family, the Nyctibiidae, consisting of a single genus with five species, confined to tropical America. They are closely related to the goatsuckers, which they resemble in their mottled plumage, capacious mouths, and small bills, but from which they may be distinguished by their manner of resting with the body more or less upright, rather than horizontal, as is usual in goatsuckers. The most widespread member of this family is the Common Potoo (*Nyctibius griseus*), a large, wide-winged bird about 15 inches long. Its intricately patterned plumage is a blending of browns, buffs, grays, black, and white, producing a general grayish brown tone. There are blackish marks on the head and back, and black spots in a broken band across the breast. The long tail is irregularly banded with blackish and grayish. The large eye is bright yellow or orange. The sexes are too similar to be distinguished with certainty in the field.

Distribution

The Common Potoo ranges over continental America from southern Mexico to Peru, northern Argentina, the Guianas, and Trinidad. In the Antilles it inhabits Jamaica and Hispaniola. We have little information on its altitudinal distribution, but older records from near Guatemala City and Tactic, Guatemala, indicate that from sea level it ascends to possibly 5,000 feet (Ridgway, 1914:592). Despite its name, this potoo is widespread rather than common and is by no means uniformly distributed in apparently suitable habitats throughout its vast geographical range. Easily overlooked by day, its nocturnal song, once heard, is unmistakable and unforgettable. In the more than 30 years since I became familiar with this song on Barro Colorado Island in the Panama Canal Zone, I have heard it in only two of the many localities where I have studied birds: near Pirapira in the Venezuelan state of Carabobo, and in the Valley of El General, Costa Rica. In the latter locality, I first became aware of the potoo, by sight rather than hearing, on 31 August 1959, nearly 24 years after I began to study the birds of this valley. Of late we have heard its voice at "Los Cusingos" in El General nearly every year, and found it nesting. My failure to discover the potoo in this valley during so many seasons in the field is the more surprising in that C. K. Underwood found it in El General on 26 July 1908 (Carriker, 1910:500). This suggests that the Common Potoo's distribution is spotty or discontinuous in time as well as in space.

Cryptic Behavior

By day, the potoo rests in open or sometimes dense woods, often near the edge, from which it sallies forth in the dusk to catch insects over clearings or neighboring bodies of water. In the daytime, it is usually seen perching at a moderate height, quite upright, with its feathers compressed, its neck stretched up in line with its vertical body and tail, and its head inclined strongly upward. Some upstanding feathers above the eyes simulate low horns, and the auriculars are puffed out. The large eyes are closed to the narrowest slits, which from time to time widen slightly to reveal what is happening nearby. In this linear, vertical posture the potoo remains quite motionless as long as it knows that it is being watched. If one moves around beneath it, the bird does nothing except to turn its head, and occasionally to shift the orientation of its body, when the observer's eyes are turned away. If, as sometimes happens, the potoo is resting on the end of an upright gray stub of the same thickness as its body, it appears to be a continuation of the stub and is difficult to detect. On any perch it looks more like a piece of dead wood than a bird.

Although the potoo is usually seen, and pictured by artists and photographers, in this vertically elongated pose, it does not maintain this cryptic attitude all day long. If you can manage to see the potoo before it sees you, you will find it still perching vertically, but shorter and stouter, with its bill directed forward rather than upward. The moment it detects your presence it elongates its body, compresses its plumage, and raises its head, all so gradually that the movement is imperceptible. If you shake its support gently, it may open its great yellow eyes and lower its head to look around, without taking flight.

The potoo's flight is swift and direct, with regular beats of its long wings, which on a downward course it may set for a prolonged glide. Viewed in flight against the night sky, it resembles a large hawk, especially a *Buteo*.

As the evening twilight deepens, the potoo stations itself on the end of a stub, an exposed branch, a fence post, or even a cornstalk, from which it flies out to catch insects, often circling broadly around and returning to the same lookout. The potoo usually captures insects in the air, flycatcher-fashion, but sometimes it plucks them from foliage, the bark of a tree, or even low herbage. I have watched a potoo weave an intricate course through the open branches of a tree in pursuit of insects. Beetles seem to be the principal food in Jamaica (Gosse, 1847), and large fireflies (*Elyta*) are favored in Trinidad (Johnson, 1937). In Hispaniola, the remains of moths accounted for 83 per cent of the food of a potoo, which had also eaten 18 locustid eggs and seven beetles (Wetmore and Swales, 1931:247).

Voice

Like its frequent neighbor, the Pauraque (*Nyctidromus albicollis*), the potoo sings chiefly in the morning and evening twilight, and by moonlight. The impression made upon us by the songs of birds, as by music of any kind, depends in large measure on the mood and setting in which we hear them. None could have been more favorable for the creation of a deep and lasting impression than those in which I first heard the potoo. Frank M. Chapman, who had written so feelingly about the potoo's voice (Chapman, 1929:262–264), had promised that I would hear it if I spent the night with him at Fuertes House on Barro Colorado Island, where both of us were then residing. This one-room cabin for occasional occupancy was beautifully situated on an elevation between two forested ravines, whence it looked down to the head of a narrow inlet, whose placid waters wound away between low, wooded ridges toward Gatun Lake.

We watched the full moon float up above the crest of the high forest and listened expectantly, but only the loud, liquid notes of a chorus of frogs broke the stillness of the night. Around ten o'clock, overcome by drowsiness, I fell asleep. In the small hours of the morning, Dr. Chapman woke me. Sitting up on my narrow cot, I looked out the window upon a night flooded with the yellow light of the declining moon, reflected in a myriad glistening points from the foliage all around us, wet from a passing shower. The frogs continued their chorus; and from the distance came, subdued yet clear, the most melancholy utterance I had ever heard from bird or beast. Although plaintive, the potoo's soft, soprano notes were so beautifully modulated that they brought to mind a phrase from Shelley's *Adonais,* "most musical of mourners." It was easy to imagine, in such a setting, that out there through the moonlit forest wandered a maiden whose lover had been snatched away by death, or, as Waterton the Wanderer had fancied long before, Niobe stood wailing for her children before she was turned to stone. *Poo-or oh oh oh oh,* the voice seemed to cry, the notes strongest at the beginning and falling away toward the end. Again and again the Poor-me-one, as the potoo is called in Trinidad, repeated its plaint. Presently, we noticed that two of them were answering each other in the distance.

More than thirty years passed before I actually watched a potoo as it sang, while sitting on its nest on the hillside behind our house at Los Cusingos. Oddly enough, although the potoo was so rare in this region and I had first heard it here only two years earlier, our cook ascribed its song to the *perico ligero* or sloth. In many other parts of tropical America, this utterance is attributed either to a sloth or an anteater. As I have heard it in Costa Rica, Panama, and northcentral Venezuela, the potoo's song varies little and has everywhere the same melancholy charm. In other parts of the Common Potoo's range, quite different calls have been ascribed to it, a matter well discussed by Smithe (1966:87). A recording by Paul Schwartz reproduces well the sweetly plaintive character of the song, and likewise how loud and piercing the opening note may sound when not mellowed by distance.

As is to be expected, the potoo sings chiefly in the drier part of the year, when it nests. On Barro Colorado, Chapman (1929) heard it almost nightly from 21 December until 3 March. After his book was published, I heard the song, with him, on 20 March 1935 and, alone, sparingly until 21 May of the same year, when the wet season had set in. In Trinidad, Johnson (1937) heard the potoo during the 10 or 15 minutes before dark on almost every evening from February until the beginning of August. At Los Cusingos, I first heard the potoo at the beginning of March 1966, six and one-half years after I first saw the bird in this region. Early the following December, it sang sparingly at nightfall, and by the middle of that month it was singing more frequently. In mid-October of 1967, when the wet season was far from ending, we heard the potoo sing at daybreak, and by early November it sang in both the morning and evening twilight. By the beginning of December, as drier weather approached, a pair was nesting close to our house. My records of the potoo's singing in this locality since 1966 are fragmentary, because of my prolonged absences.

Nest Site and Egg

In the drizzly evening twilight of 9 November 1967, I heard the song of a potoo. Then a large, dusky bird, evidently the one I had heard, alighted in an aguacatillo tree (*Persea Skutchii*) in the hillside pasture behind our house at Los Cusingos. It rested on a thick, nearly upright branch at a point where it bent to one side, so that the bird, holding itself quite erect, appeared to be a broken-off stub. After a minute or so, the potoo flew to a dead guava tree higher on the slope and perched upright on the end of an ascending stub about as thick as its own body. In the dim light, I could hardly distinguish it from the broken-off branch; until the bird flew away and the branch suddenly grew shorter, I was not sure it was there. While the potoo rested on this stub, another flew up and tried to alight beside or upon it but, not succeeding, continued over the brow of the hill and out of sight.

These potoos were evidently selecting a nest site. On 1 December, and again on the following day, a potoo was resting in the aguacatillo tree every time I looked. I did not disturb it, and when it spontaneously left in the evening twilight of 2 December, I saw that it had been covering an egg, in the exact spot where the potoo had alighted three weeks earlier. The single large egg rested, at a height of about 30 feet above the ground, in a depression so shallow that more than half the egg was exposed above the rim. This knothole was situated at a sort of elbow in the thick, almost vertical main branch, which bent to the other side, then curved upward again, so that it did not interfere with the incubating bird.

As in all reported nestings of potoos, only one egg was laid. It seemed so precariously lodged in its shallow depression that I did not try to reach it. Viewed from the hillside above the nest tree, where I was not far below it, the egg appeared white, with faint markings. According to F. Haverschmidt (*in* Thomson, 1964:662), the eggs of *N. griseus* are oval and white, without much gloss, and are sparsely marked with rather small lilac and brown spots. Eggs from Trinidad measured 41.5 by 32.0 millimeters, from Brazil 36.2 by 29 mm, and from Surinam 35.9 by 26.1 mm. Eggs have been found in Trinidad in April and August, in Surinam in April, and in Brazil in November and December. A nest, 60 feet up in the forest on Trinidad, was reported by Johnson (1937). There appears to be no previous record of a nest of the Common Potoo in Central America, but Van Tyne (1935:20) published a photograph of a juvenile found on the leafy floor of high forest in El Peten, Guatemala, on 5 May 1931.

The nest I found in the very open crown of a medium-sized tree growing on a grassy hillside was clearly visible from 100 yards away. From the back of our house we could see the potoo sitting on it, even with the naked eye, while through field glasses we could follow its movements. By night, in the beam of a flashlight, its brilliant orange eye-shine revealed its presence from afar. For nearly three months we watched this nest, sometimes from our dooryard, sometimes while standing or sitting on the hillside close by it, and during several night-long vigils. Our near approach, whether by day or night, appeared to have no effect upon the potoos other than to send them into the elongated alarm posture, from which, if we watched quietly, they soon relaxed. Throwing the beam of a flashlight upon them in the darkness of the night did not interfere with their activities, such as feeding the nestling.

Incubation

We could count upon seeing a potoo covering the egg at any hour of the day or night, except for a brief interval at dawn and a longer period at the beginning of the night. Although we made no day-long watch, we spent much time in view of the nest without witnessing a change-over or ever seeing a second potoo anywhere in the vicinity in full daylight. I have no doubt that the same individual remained continuously on the egg all day long. I watched through the night of 16–17 December, when the moon was full, but unfortunately hidden much of the time by clouds, which before dawn covered the whole sky darkly. Since the nest tree was silhouetted against the sky, I believe that I should have noticed a change-over even while the sky was overcast, but I saw none. Evidently the nocturnal session, like the diurnal session, was continuous.

In the earliest light of dawn, while the stars still shone brightly, the potoo which had incubated through the night flew from the nest, usually going down the hillside toward the river. This morning departure occurred from 05:00 to 05:06 on nine mornings between 3 and 18 December; but when I resumed observations at the beginning of January, toward the end of the incubation period, it took place, on three mornings, between 05:12 and 05:18. The egg remained exposed, in the dim light, for from 0 to 15 minutes; for 11 mornings, the average period was 7.6 minutes. While the brighter stars still shone and the first tints of dawn were suffusing the the eastern sky, a potoo flew up and settled on the egg. Since the sexes were indistinguishable, I could not tell whether this was the bird that had left a few minutes before or its mate. The brief interval of neglect, sometimes only one to four minutes and evidently too short for a potoo to satisfy its hunger after an all-night fast, favored the view that the other had come to take charge of the egg. This was certainly the case on 2 January, when at 05:14, standing only 50 feet away in full view, I witnessed the only change-over that I saw during the period of incubation. On this occasion, the sitting potoo did not leave until its mate, flying up swiftly through the twilight, was almost on top of it. The egg was left uncovered for only an instant, the newcomer settling on it the moment the other departed, never wavering in its swift, smooth approach until it came to rest on the egg.

It was certain, then, that both sexes incubated, one sitting by night and the other through the day. The daytime shift began at times ranging from 05:04 to 05:23 and lasted from 12.50 to 12.75 hours. The potoo that incubated all day nearly always flew from the egg in the rapidly fading light between 17:45 and 17:50, rarely a few minutes earlier or later. With two exceptions, the hour of departure on 29 evenings fell between 17:42 and 17:54. One of these exceptions occurred on 11 December, the first clear afternoon and evening in many days. Then the potoo left its egg, enticed away by a passing insect, at 17:38. After catching the insect, it continued to a neighboring stub, where it stretched and preened. It returned to the egg at 17:45, and 10 minutes later it left again for a longer absence. On 12 December, a dark and drizzly evening with flashes of distant lightning, the potoo remained incubating until 18:22. On the rainy evening of 17 December, the potoo did not leave for its customary crepuscular outing, but evidently remained until its mate replaced it in the darkness. On a number of evenings, I noticed that the potoo left its egg from one to eight minutes after the Pauraque began to sing.

After the evening departure, the egg remained exposed for 45 to 95 minutes, usually for about an hour. On 27 December, when the potoo left at 17:47, the egg was already covered by 18:32. At the other extreme, on 4 December the diurnal session ended at 17:48 and the nocturnal session did not begin until 19:23. At the nest studied by Johnson (1937) in Trinidad, the egg was left exposed for "many hours" after darkness fell. Usually, especially during the latter half of the long incubation period, the potoo taking the night shift at our nest arrived before 19:00. The return to the nest displayed admirable control of flight. With amazing precision, the potoo flew right into the incubating position, folding its wings as it alighted. After it came to rest, no further adjustment to the egg seemed necessary.

The potoo always incubated facing into the supporting branch, with the long axis of the body vertical, the base of the abdomen covering the single egg, and the end of the long tail touching the branch below (Figure 1). When the bird was at ease, its body was contracted, with the feathers fluffed out making it appear stout, the head horizontal, and the minuscule bill inclined somewhat downward. At times the potoo fluffed out its ventral feathers so far that I was sure they hid a nestling, although the egg had not yet hatched. The potoo's eyelids moved continually, like those of an incubating Pauraque, opening the merest slit, then closing tightly for a moment, then opening a trifle, rarely revealing much of the large yellow eye. Evidently a scarcely discernible opening was quite wide enough for the potoo to see what approached. The sparsely foliaged tree afforded scant shade, and much of the time the incubating potoo sat in strong sunshine. Sometimes it panted with its huge mouth slightly open. Or sometimes it assumed a more inclined posture, its long tail slanting outward from the trunk, its wings half-spread laterally, apparently sunbathing, after which it sometimes preened. Beneath a hard shower, the potoo sat with its body contracted and plumage fluffed out.

The visible approach of anything larger than a small bird caused the incubating potoo to compress and elongate its body, at the same time raising its head until it inclined strongly upward in alignment with the body and tail. The eyes were closed to the merest slits. The change from the plump resting posture to the slender alarm posture was slow and steady rather than abrupt, taking about 10 to 15 seconds. Since rapid movement is always revealing, a too hasty change of attitude would have defeated the very function served by the

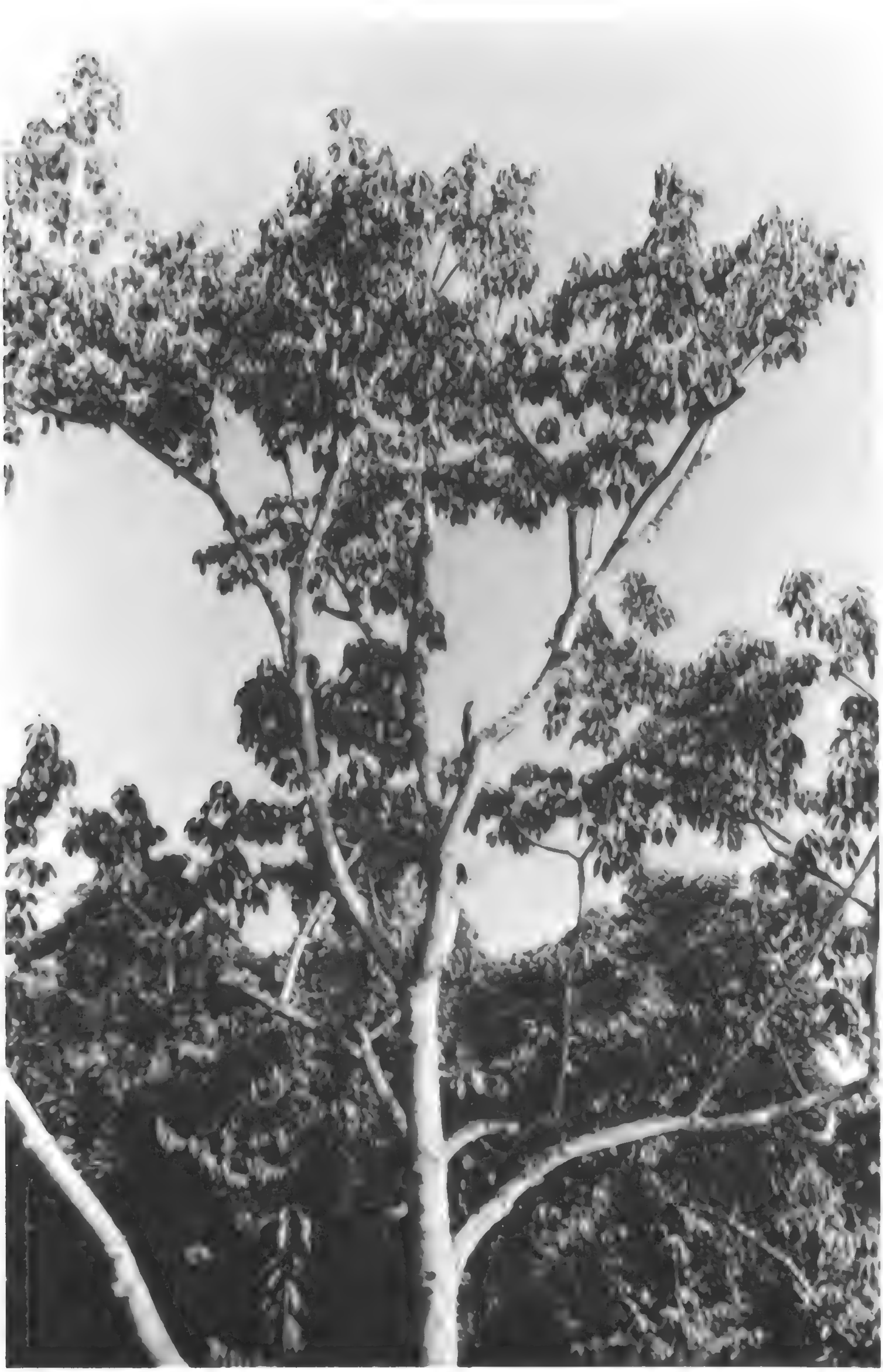

Figure 1. A Common Potoo incubating in full alarm posture in an aguacatillo tree at El Quizarra, Valley of El General, Costa Rica, December 1967. Photograph by the author.

cryptic posture. The bird's readiness to assume the alarm posture while incubating varied greatly with circumstances. In full daylight it reacted most readily to the sight of any moving object: a man walking at a distance, a Turkey Vulture (*Cathartes aura*) or a Broad-winged Hawk (*Buteo platypterus*) flying overhead, would cause it to stretch upward to its full length. In the morning or evening twilight, the potoo often stretched upward only partly, or not at all, when I approached; and in the beam of a flashlight at night, it often retained the contracted posture. However, there were exceptions, and on moonlit nights my approach to the base of the nest tree might make the sitting bird elongate itself fully. Once, after the nestling hatched, I saw the brooding parent suddenly stretch upward into the alarm posture at 03:00. My flashlight beam picked out the eye-glow of some small animal, probably an opossum, in the roadway 50 or 60 feet below the nest. As the animal moved farther along the road, the potoo sank down to the resting posture, which it maintained when, a little later, a skunk rummaged on the slope below the nest.

As the potoo was most ready to assume the alarm posture in full sunlight, so it then took longest to resume the resting posture. When, after walking beneath the nest to make the bird stretch up, I watched through binoculars from a distance of 50 yards or so, it might require nearly a quarter of an hour to return to the resting attitude. In the evening, if I stood close beneath the nest, perhaps waving my arms to make the potoo elongate itself fully, it might resume the resting posture in as little as 2.5 or 3 minutes, while I sat watching in full view on the hillside scarcely 50 feet away. Even when most rapid, the contraction of the elongated body was imperceptibly slow.

Sometimes at sunset I found the potoo drowsing on the egg in a very contracted posture, seeming about two-thirds as long, and twice as fat, as when in the full alarm posture. As the light faded, it became active, opening its big yellow eyes, turning its head from side to side to look around, yawning cavernously, stretching its broad wings alternately sideways or both together above its back, spreading its tail, preening, perhaps giving once or twice a subdued version of its song, consisting usually of not more than four notes. Tempted by some insect that flew past or crawled over a neighboring branch, it sometimes darted out to seize the creature that I could not see, then returned immediately to its egg—a momentary absence that I did not consider to terminate the long diurnal session. The potoo did not perform all these activities every evening, but a selection of them.

Finally, as the twilight deepened, the bird left, falling away from the egg. Often it went to alight on a neighboring dead stub of a cecropia tree, into which a female Red-crowned Woodpecker (*Centurus rubricapillus*) had already retired for the night. Here it occasionally repeated some of the activities that had preceded its departure from the egg, such as stretching, preening, and calling briefly, or it performed other activities that it had omitted to do at the nest. Soon it flew off beyond sight, toward the forest or the river. Rarely its mate appeared at this time; but it was exceptional to have two potoos in view at any hour of the day or night, until after the egg hatched. Throughout the nesting, I scarcely heard any song from either parent, except the few notes uttered just before its departure at nightfall or daybreak.

I never saw a potoo turn the egg, or even touch it with its bill. To do so might have dislodged the egg from the shallow depression. Toward the end of the incubation period, I noticed a conspicuous dark spot on the shell—either dirt or a marking—that was always in the same orientation. I never chased the potoo from its nest in order to see whether the egg had hatched. Indeed, to do so might have been difficult, for later, when the nestling was a few days old, a parent continued to brood it, in the full alarm posture, while we encircled the trunk with a wide band of sheet metal to prevent predatory animals from climbing up. Driving nails through the resounding metal was necessarily a noisy operation.

The potoo's departure at dawn on 4 January revealed the egg still intact; the evening departure on the same day disclosed a downy nestling. Since I had first noticed the egg on 2 December, the incubation period at this nest was 33 days or more. Johnson (1937) found that the incubation period of an egg in Trinidad was 29 or 30 days.

The downy nestling faced inward, toward the ascending branch, and behind it lay the larger part of the empty shell, with a very jagged edge. Could the shell have been glued to the stub, perhaps with saliva, so that the egg would not fall? By the following evening, the shell had vanished from the nest, and I looked in vain for fragments on the grass beneath.

The Nestling

Development

The newly hatched potoo was everywhere densely covered with short, whitish down. It already rested facing inward, as the parents did when they incubated or brooded, an orientation that it rather consistently maintained through nearly all of the long nestling period. It soon developed a decidedly prognathous physiognomy, with a tiny bill at the end of a conically projecting mouth covered with whitish down, like the rest of its body.

On 15 January, when the nestling was 11 days old, I first noticed its eyegleam, which was still faint. At this age, too, I became aware of its voice, a sort of hoarse buzz, uttered when it was fed. On 20 January, when 16 days old, I first saw it flap its stubby wings in the twilight. The nestling now showed more brown on the back and wings, and dark shaft streaks on the ventral feathers. The next day, when for the first time I found it alone in full daylight, it sat upright, with its head drawn in, in much the same posture as the parents assumed when drowsing on the nest. It did not change its attitude at my approach; but when I stood directly below the nest and made a noise, it stretched up its body and elevated its bill to an angle of about 30 degrees from the horizontal, foreshadowing the alarm posture of the adults but not assuming it fully. It maintained this posture for only a brief interval. When the nestling was 19 days old, I found it resting in front of its parent on the nest. As I came near, the parent stretched up in the alarm posture and the young bird did the same. Its rudimentary tail now projected over the edge of the stub.

On 30 January, when the nestling was 26 days old, its wing coverts and tail feathers were appearing through the abundant down that still covered its body. Feathers were forming "horns" above its eyes. It assumed the alarm posture only in response to a stronger stimulus—a closer approach or a noise—than the adults reacted to, and it did not elongate itself so pronouncedly. On this day, I first saw it away from the knothole where it hatched. It had climbed about one foot up the thick ascending branch beside the nest and rested there in its customary upright posture. In the evening, it returned to its usual place. When it stretched and flapped its wings in the evening twilight, I noticed that its remiges were expanding, but when the wings were folded they were concealed by the downy covering of the body.

By 8 February, when 35 days old, the nestling was well feathered with a juvenal plumage similar in pattern to that of the adults—even to the dusky malar stripes—but much lighter in general tone. The "horn" above each eye was now quite prominent. I had not again seen it climb up the branch beside its nest. By night it was inactive, except at mealtime.

By 18 February, the 45-day-old nestling was becoming more active. Late in the morning it rested on the ascending branch about two feet above the nest—higher than I had seen it before—and it stayed there all afternoon. As it grew dark, the young potoo stretched its wings alternately, flapped them a little, then sidled down the branch to the nest. Here it flapped its well-developed wings vigorously. It repeatedly seemed to pick something, perhaps bits of bark or lichen, from the branch and eat it. When a parent came with food, it made the harsh buzz. Two days later, it took its first short flight.

Brooding

For the first two weeks of its life, the nestling was brooded most of the time, day and night. It was left alone chiefly during the first hour of the night, when the egg had been left uncovered, and more briefly as the night ended. Thus on 4 January, the day it hatched, the nestling remained exposed for 34 minutes, from 18:13 to 18:47. In the next few nights, when both parents were bringing food, the nestling was left alone for periods rarely exceeding 15 minutes.

My son and I watched continuously through the night of 14–15 January. The moon was full, but the sky overcast much of the time until midnight. At 18:01 the parent who through the day had brooded the 10-day-old nestling left for the first time. From then until 19:05 the nestling was brooded only twice, for 2 minutes each time, and left exposed three times, for 2, 22, and 36 minutes. Then, from 19:05 until 05:12 next morning, or through the greater part of the night, it was brooded continuously. In the early dawn the nestling was left exposed for 3 minutes, brooded for 5 minutes, then left exposed for 4 minutes, after which a parent settled on the nest for the day, at 05:24. From the beginning of activity by the potoos at 18:01 on 14 January to its cessation in the waxing daylight on 15 January, the nestling was left uncovered only 67 minutes, during which it was frequently fed. Both parents brooded, and in the course of the night we saw them change-over five times. Spells of brooding by one parent ranged from 2 to 234 minutes. Johnson (1937) believed that the young potoo was "never left exposed" during the first three weeks of its life.

At first, the brooding parent always sat facing inward, as it had incubated, with the nestling in front, covered by its abdominal feathers. As the nestling grew larger and stood erect, it formed a bulge in front of the parent that was especially abrupt and noticeable when the adult became tall and slender in the alarm posture. When the nestling was 12 days old, I noticed its head protruding from the parent's feathers for the first time in full daylight. Through much of the following day, the parent brooded facing sideways, having rotated about 90 degrees from its usual position, and the nestling had turned the same way, since it usually faced in the same direction as its brooding parent. Now its ventral surface as well as its head was exposed, but feathers of the parent's abdomen covered its sides.

Early in the afternoon of 21 January, I saw the nestling, now 17 days old, alone for the first time in full daylight. During the next week, however, I always found a parent on the nest in the daytime, often with the young bird resting in front rather than within the adult's plumage. On 28 January, a parent accompanied the nestling much, if not all, of the day; but on 29 January, when 25 days old, it was alone, as thenceforth we always found it, except when it was fed, until its departure nearly a month later. The last time we saw a parent brooding in darkness was on the night of 22–23 January. Long before diurnal brooding ceased, the nestling seemed to have enough plumage to keep it warm on mild January days. Probably the chief service rendered by the attendant parent was to shield it from the strong sunshine, for the aguacatillo tree was rapidly shedding its foliage. Moreover, the parent had better protective coloration than the nestling, whose plumage was too pale to match the bark of the nest tree, although it was scarcely lighter than some of the dry lichens that encrusted it.

Feeding

I first saw the nestling when, in the evening twilight of 4 January, the parent which had covered the nest through the day flew out to seize a passing insect in the air, then at once returned. Twice more the parent flew out to catch insects, once from the air and once from the foliage of the nest tree, each time returning to the nest. After its third return, it bent over to feed the nestling, which stuck its head out from its parent's abdominal feathers to receive its first meal. The parent made jerky movements with its neck, as though regurgitating, and seemed to feed the nestling several times more. Between feedings, the nestling mostly stayed out of sight, although occasionally the tip of its bill projected from the parent's abdominal feathers.

At 18:13, much later than while it incubated, the parent flew away through the dusk. The nestling remained alone until 18:47, when a parent flew up and brooded it. At first the adult seemed to be disturbed by the beam of my flashlight, but soon it moved its neck as though regurgitating and bent down to feed the nestling, which stuck its head out as before. The feedings continued for about five minutes, but in the flashlight's beam I could not see the details as well as I wished. After the series of feedings, the parent sat quietly brooding in the light of the crescent moon.

Next morning I resumed watching at 05:00, when the east was brightening, and continued until 05:35, when there was much daylight. One parent stayed continuously on the nest, save for three momentary sorties to catch insects. After the last, it fed the nestling once, then settled down to brood through the day.

That evening, as daylight faded, the nestling, not yet a day and a half old, stuck its head through the feathers of the brooding parent's abdomen, as though expecting a meal. A day later, it could stretch up so far that the parent, standing erect in the brooding attitude, needed to bend down little to reach its mouth. The nestling turned its head sideways to receive the food. Until the end of the nestling period, the young potoo was always fed while standing in front of the parent on the nest and facing in the same direction as the parent. At first only its head projected from the parent's feathers. As it grew, its whole body was exposed.

During the succeeding days, the delivery of a meal became more rapid. Although on the first evening a feeding had continued for about five minutes, from the second until the ninth evening it lasted only about two to four seconds. When the nestling was 10 days old, the delivery of a meal rarely took as long as a second or two. From the nestling's second to sixteenth day, a parent returning with food occasionally delivered it in two or even three installments; but during the second half of the nestling period, the meal was always delivered all at once. Alighting on the nest with the nestling in front of it, the parent alternately stretched and contracted its neck, regurgitating what appeared to be a large mass of compressed insects. To pass this to the nestling took only an instant, after which the parent flew away, a fraction of a minute after its arrival.

From at least its eleventh day onward, the nestling uttered a hoarse buzz at mealtime, often beginning as its parent approached and continuing after it had received the food and retired into the parental feathers or, at a later age, until after the parent left. The hungrier the nestling appeared to be, the more it buzzed. This sound helped us to detect the feedings on dark nights, since we did not keep the flashlight beam trained on the nest continuously, but only occasionally and at mealtime.

During the nestling's first 10 days, it received from three to six meals during the parents' first hour of activity at the beginning of the night, and as many more in the 15 or 20 minutes between the first dim light of dawn and fairly bright daylight. After this, the number of feedings in each of these intervals was reduced to one or two. On the night of 14–15 January, when the moon was full but unfortunately obscured by clouds much of the time until midnight, the parents fed the nestling 15 times between sunset and sunrise, delivering eight meals before midnight, seven after midnight. During the night of 8–9 February, when the waxing moon set at about 01:30, the nestling received only 10 feedings, eight before midnight and two after midnight, when beneath a clear, starry sky the air had become uncomfortably chilly. We had abundant evidence that both parents fed the nestling, although it was impossible to learn their separate roles.

Sanitation

We never saw a parent remove a dropping, which it could hardly take in its bill without hovering beside the nest. Some deposits on the herbage and fallen leaves beneath the nest tree suggested that the nestling shot its droppings free of the supporting trunk, probably while the parents were absent, but we never saw this act.

Departure

On the afternoon of 20 February, the young potoo, now 47 days old, climbed up the slanting branch above the nest. As it grew dark, the young bird alternately stretched each wing broadly, then sidled down to the nest, where it again stretched its wings and flapped them vigorously. It seemed to pluck things from the bark, and it looked around much, as though seeking a place to which it could fly. Then, at 18:07, in deep twilight, it launched forth on its first recorded flight. After going only a few yards, it circled around and alighted on a neighboring upright branch with a lateral projection, in a site quite similar to that of the nest and only a few feet distant from it. Here it plucked lichens, liverworts, or bits of bark and swallowed them, as was evident from the movements it made. It did this again and again, as though hungry. Ten minutes after the juvenile's flight, a parent silently arrived and alighted on the nest. The young potoo set up its hoarse buzz and continued until the parent flew across and fed it while standing behind it, in the usual manner, then flew away. A few minutes after this meal, the first we saw it receive away from the nest, the juvenile flew back to the nest, where it flapped its wings vigorously while clinging to the branch, then settled down to pass the night there. Its eye-shine was now only slightly less brilliant than that of the adults', but somewhat more yellow, less orange.

Each evening the young potoo became more active and took longer flights. On the evening of 22 February, it made six flights before receiving its first meal. All were between branches of the nest tree itself, the longest about 20 feet, from one side of this tree to the other. Sometimes the young potoo headed outward, as though to begin a longer journey, but after going a few yards it circled around and returned to its natal tree.

After passing the night of 22–23 February on the nest, the young potoo flew at dawn to the similar site a few feet away. Here it passed the day. This was the first time I saw it in full daylight away from the branch on which it had hatched.

On the evening of this day, the juvenile made 14 flights in the 15 minutes before it was fed. Some of these flights were short, between the nest and the branch just a few feet away where it had passed the day — two points of attraction between which it now frequently alternated. But at times the fledgling flew far out from the crown of the tree, 40 or 50 feet, only to veer around and alight on a branch of the nest tree. Once it flew halfway around the tree's crown, to enter it from the opposite side. It never alighted anywhere except in the aguacatillo tree in which it grew up. I could not learn whether it caught insects on any of these flights. At the various points where it alighted, it plucked many things from the bark, as on previous evenings. There was the usual stretching, shaking itself, and preening. Finally, the young potoo settled on the nest for its last night there.

As the first promise of dawn brightened the sky above the eastern horizon on 24 February, the young potoo became active, sidling up the branch beside the nest and appearing to pluck things from it. At 05:04 a parent fed it on the nest. As the undersides of the eastern clouds became tinted with rose, it flapped its wings and picked more things from the bark. After another meal, it flew to the next branch, then made three long, circling flights, out from the nest tree and back again. Finally, at 05:30, it flew out once more. Now for the first time it did not turn back, but continued across the road and down the hillside into light second growth woods, where it vanished. After breakfast I spent a long while vainly seeking it.

The young potoo flew away while the parents were out of sight. How would it establish contact with them? Would it return to the nest to be fed? That evening I watched in a slow drizzle. In the gloaming at 18:17, a parent alighted on the nest, as though expecting to find its offspring there. After delaying a short while, it flew to the nearby cecropia stub from which it had often caught insects. Then it went to other exposed perches, and twice more it came to the nest. Several times it called in its soft, melodious voice. Finally, 10 minutes after its arrival, it flew down into the woods where the young bird had disappeared at daybreak. Possibly it had heard the juvenile's voice, although I failed to detect it.

Soon a potoo, probably the other parent, alighted on the nest. After flying around a while, but not calling, this one also flew to the woods to which the fledgling had gone. So it probably received its supper – or, more properly, its breakfast – despite its departure without its parent's knowledge. I never saw it again.

If we count from hatching to the first time the young potoo was seen elsewhere than on the nest or the branch beside it, the nestling period was 47 days (4 January to 20 February). If we count from hatching to its departure from the nest tree on 24 February, the nestling period was 51 days. Adding at least 33 days for incubation, the period of occupancy of the nest becomes no less than 84 days. This is a long time for a vulnerable bird and its defenseless young to remain on an exposed stub or branch of a tree in or near tropical woodland where predators abound; it speaks eloquently for the protective value of the potoo's "dead stub" pose. With the exception of the Black Vulture (*Coragyps atratus*), no other land bird that I have studied in tropical America, not even excepting hole-nesters, has such long incubation and nestling periods. The young potoo studied by Johnson (1937) in Trinidad remained on the nest tree only 40 days.

Since this nesting had terminated successfully so early in the year, long before most birds had started to reproduce, I thought that it might be followed by a second brood. Although we have checked carefully, we have never seen a potoo sitting in the nest tree again, either in that season or the following years.

Summary

By day, the nocturnal Common Potoo (*Nyctibius griseus*) often rests on the end of a stub, from which it is difficult to distinguish in its thin, vertically elongated alarm posture. When at ease, it assumes a shorter, stouter figure.

Its food consists of moths, beetles (including fireflies), and other insects, caught in its great mouth on flycatcher-like sallies from an exposed perch, to which it often returns.

The song, consisting of a descending series of soft, plaintive notes, is heard in the evening and morning twilight, and by moonlight, chiefly in the drier part of the year.

At the beginning of December, in the Valley of El General in Costa Rica, a single whitish egg was laid in a knothole 30 feet up on a stout upright branch of an open-crowned tree growing on an exposed hillside. The egg rested in a depression so shallow that the greater part was exposed above the rim.

Both parents incubated, covering the egg continuously except for an interval not exceeding 15 minutes at daybreak and a longer interval of 45–95 minutes at the beginning of the night. The only observed change-over occurred at dawn, and both the long nocturnal session and the even longer diurnal session appeared to be continuous, and by different parents. They apparently never turned nor touched with their bill the precariously situated egg. The incubation period was at least 33 days.

The newly hatched potoo was densely covered with whitish down. From the first, it rested facing the supporting branch, just as the parents did when they incubated or brooded. At the age of about 17 days the young bird assumed, imperfectly, the vertically elongated alarm posture, but it did not display the full alarm posture until some days later. At the age of 26 days, it was first seen resting on the branch above its "nest," and thereafter its excursions over the neighboring boughs gradually became longer. When 35 days old, it was well feathered, much in the color pattern of the adults, but in a lighter tone.

During its first two weeks, the parents brooded the nestling most of the time, leaving it alone chiefly during the first hour of the night and more briefly at dawn. The brooding parents changed over five times in the course of a night. Nocturnal brooding ceased when the young potoo was 19 days old; but, with rare exceptions, a parent attended it all day until it was 25 days old, after which it was always alone, except when being fed.

The nestling was fed by regurgitation. Its first meal lasted about five minutes, but gradually the time devoted to transferring food shortened, until, during the second half of the nestling period, the parent took only an instant to deliver what seemed to be a large mass of compressed insects. When 10 days old, the nestling was fed 15 times, by both parents, between nightfall and daybreak on a night when the moon was full. When 35 days old, it received 10 meals in the course of a night when the moon was waxing. From about its eleventh day onward, the nestling always uttered a hoarse buzz when a parent came to feed it.

The severance of the nestling's ties with the nest was gradual. During its last days in the nest tree, it climbed over neighboring limbs, stretched and flapped its wings, flew from branch to branch, and even took short circling flights out from the nest tree and back again. These exercises took place chiefly in the evening twilight, when, before its first meal, it frequently plucked and seemed to swallow lichens, liverworts, and fragments of bark. The nestling's first recorded flight of a few yards occurred when it was 47 days old. Before sunrise on its 51st day, it finally flew from the nest tree to the neighboring woods and was not seen again.

From the laying of the egg to the young potoo's departure, at least 84 days elapsed. The survival of the exposed "nest" for so many days convincingly attests the protective value of the potoo's dead-stub pose. While incubating or brooding undisturbed, the parent sat in the rotund contracted posture; but a man approaching, a large bird flying overhead by day, or a small mammal prowling beneath the nest in the night, made it stretch up into the slim alarm posture. After the disturbance had passed, the resumption of the contracted posture took as long as a quarter of an hour in bright sunshine, but only two or three minutes in the evening twilight. Although the movement of elongation was much more rapid than that of contraction, it was nevertheless imperceptibly slow.

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Keith Shackleton.

Cape Petrel, *Daption capensis*. Drawing by Keith Shackleton.

THE LIVING BIRD

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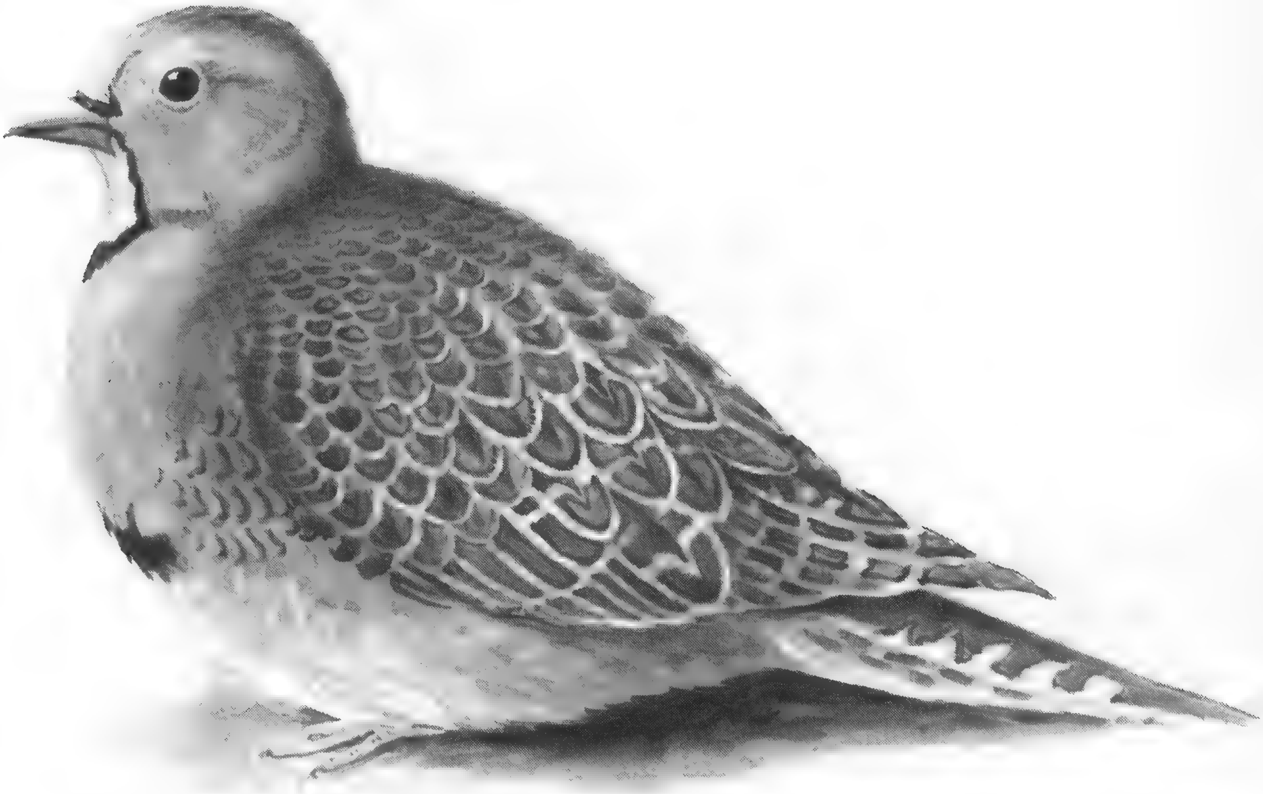
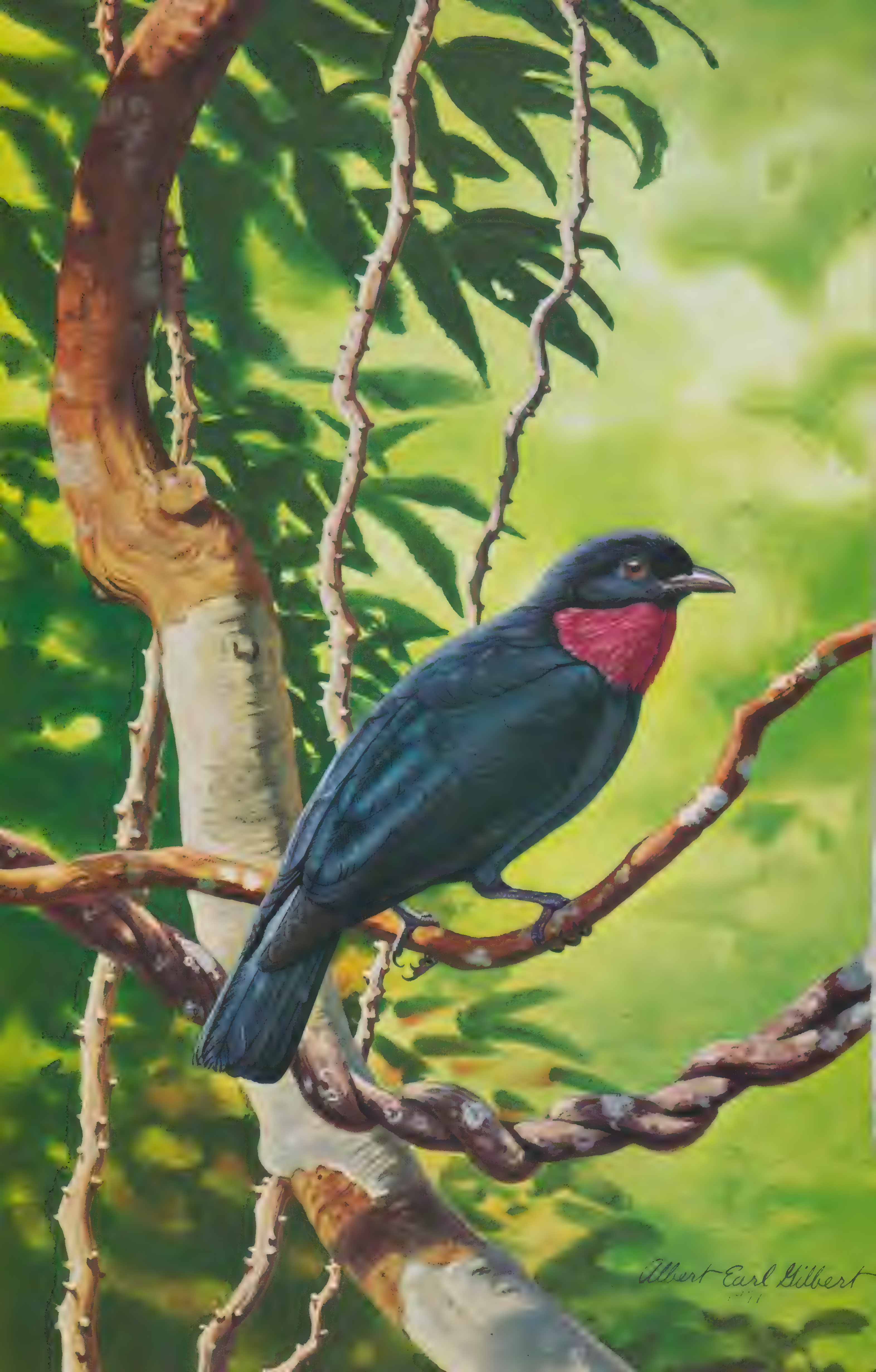


Gray-breasted Seedsnipe, *Thinocorus orbignyianus*. Painting by George Miksch Sutton.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OBSERVATIONS ON THE PURPLE-THROATED FRUIT-CROW IN GUYANA

D. W. Snow

The Purple-throated Fruit-crow (*Querula purpurata*) belongs to one of the many monotypic and isolated genera included in the diverse family Cotingidae. About the size of a jay, it has short legs and long, broad wings which, when folded, reach nearly to the end of the tail. A steel-gray beak, widest at the base and hooked at the tip, gives the broad head an almost trogon-like appearance. The plumage is entirely black, except that the male has a triangular throat-patch of glossy crimson feathers of modified structure (Strong, 1952). The throat-patch is spread and fanned out laterally by the male in display, and the same feathers, though black and less conspicuous, are spread by the female also.

Although this species is widely distributed and, in some places, quite common from Costa Rica south through the tropical forest areas of South America, no detailed observations appear to have been made. Most observers have noted that it goes about in small flocks: Slud (1964) refers to groups usually of from three to several individuals in Costa Rica; Chapman (1929) reported parties of from six to eight birds in Panama; and Olivares (1958) mentions bands of from four to six birds in Colombia. The records also show that its food consists of fruits and large insects, typically plucked or picked from the vegetation in flight.

Two ornithologists have found nests. Ellis (1952) reported a male and female cooperating in building a nest about 75 feet up in a tree at the edge of a clearing on Barro Colorado Island, Panama. Later he saw the female incubating, but could obtain no further details. Haverschmidt (1968) found a bird sitting on a nest 65 feet up in a leafless tree on the edge of a forest in Surinam, and, on another occasion, watched a male building. The nests as described by both Ellis and Haverschmidt were insubstantial, open cups.

I had opportunity to study fruit-crows from 16 January to 6 April 1970 when I camped in a forest clearing in the foothills of the Kanuku Mountains in southern Guyana. We had one fruit-crow nest that was built less than 100 yards from our camp and was successful and another about half a mile away. I devoted 85 hours to watching the first nest, five hours to the second, and made daily observations on the birds themselves that frequented the camp clearing. I also made incidental observations on other fruit-crows, all within two miles of camp.

Purple-throated Fruit-crow, *Querula purpurata*. Painting by Albert Earl Gilbert.

Social Organization

Parties of fruit-crows are not simply feeding flocks or loose associations, as might have been supposed from earlier reports. They are closely integrated social groups which not only feed, rest, preen, and almost certainly roost together, but also jointly attend a single nest. F. Gary Stiles (pers. comm.) found a group of Purple-throated Fruit-crows in Costa Rica roosting side by side in close contact with one another.

The group that attended the nest near our camp consisted of four birds: two adult males, a female, and another bird in female plumage except for two red feathers on one side of its throat. The other group, nesting about half a mile away, consisted of a male and two birds in all black plumage, of which one, and probably both, were females. A third group, which we saw only occasionally, consisted of two males and a female and, possibly, a second female which may have been out of sight on a nest. We watched other groups of three or four birds farther afield; but it was usually difficult or impossible in such cases to be sure that we had seen all the birds because we found the groups in the tops of trees in high forest without clearings. About half a mile seemed to be the average distance between groups. On a two and a half mile walk, that I made several times between camp and a cock-of-the-rock display ground up the valley, I regularly passed within sight or sound of four or five groups of fruit-crows.

The social bonds between the individuals in a group are extremely close, and there is almost no aggression between them. At least this condition prevailed in the group near the camp and seemed to be true of other groups that we watched less thoroughly. In the camp group, the two males maintained a stronger social bond with each other than with the nesting female. The two males often perched side by side, sometimes almost touching, and occasionally preened each other. During the second half of the study, Male B lost a central tail feather and so was distinguishable from Male A.

Male A was the dominant bird, or more appropriately, because we saw no aggression, the "leader" of the group. When the group moved from place to place, Male A initiated the move. He associated with Female A more closely than did the other male, and he attended the nest more assiduously. The fourth bird — I refer to it as Female B although I never definitely ascertained the sex — was the most detached of the group. She nearly always trailed behind the others when the group moved, and she tended to perch a little apart from the others. Her unobtrusive behavior may have been partly due to the fact that she was in wing molt during nearly the whole of the period of observation.

The members of the group maintained contact with one another by frequent, and at times almost continuous, calling which normally ceased when all members of the group perched together, resting. The group near camp ranged over an area about 250 yards long, mainly along the stream that flowed past their nest tree and our camp. They did not, it seemed, range far up the slopes on either side of the valley, where the forest was drier and poorer; or if they did, they could not have spent much time there because we found them so regularly along the valley bottom. The neighboring group occupied a stretch of valley at least 350 yards long, but we did not determine the limits of their area. We never saw any interactions between the two groups at their mutual border. Most of the time they stayed well apart from each other.

Food

Purple-throated Fruit-crows usually feed in a manner typical of many cotingids — by seizing their food, both fruits and insects, in flight; but they regularly perched to pluck the fruits of *Didymopanax morototoni* and *Guarea trichilioides,* both of which bear their fruits in large bunches on strong stalks that afford a foothold.

They search for insects by perching quietly and scanning the vegetation around them, often bending low, twisting the neck, and turning the head. In 81 observations of fruit-crows taking food, the fruit-eating records were two and a half times as numerous as the insect-eating; but as soon as we knew the main fruit trees near the camp, the fruit-eating was much easier to see and record. Thus our data are undoubtedly biased. It is clear at least that both fruit and insects are of comparable importance in the diet. They took the fruits most often around the middle of the day, perhaps because they needed liquid at this time. The food taken to the young in the nest, which I shall discuss later, consisted almost entirely of insects.

We listed eight different kinds of fruits eaten by fruit-crows between 17 January and 3 April. Certainly, these eight were the main ones taken in the immediate area of camp, since all but three of the seeds collected in a tray slung beneath the nest were from trees at which we saw the birds feeding. The four main fruits, which comprised 90 per cent of the fruit-eating records, were:

Didymopanax morototoni (Araliaceae)	17 January–8 March
Guarea trichilioides (Meliaceae)	17 January–18 March
Hirtella sp. (Chrysobalanaceae)	21 February–8 March
Lauraceae sp.	12 March–3 April

In addition, the fruit-crows fed on the fruit of *Cecropia* sp. (Moraceae) during the latter part of our study period. They also took another species of Lauraceae early in the period, and a few times they ate two kinds of unidentified fruits. The largest fruits were lauraceous, the early fruiting species measuring about 27 × 15 millimeters.

Voice and Displays

The usual call, uttered repeatedly whenever the birds are active, is a mellow, disyllabic *oo-waa,* delivered with the beak closed and the throat feathers more or less fanned. This is the call that gives the bird its local names—"ter-wo" in the Kanuku Mountains and "cuaba" in western Colombia (Olivares, 1958). When uttering this call, the bird typically leans forward nearly horizontally and shivers its partly fanned tail in a curious side-to-side movement which, as Chapman (1929) remarked, gives the impression that the bird is shaking water out of its tail feathers. It frequently intersperses the disyllabic call with a monosyllabic, more drawn out *wooo* with an upward inflection.

The fruit-crow also utters a variety of harsher calls with the beak open. Frequently, when the birds are feeding or moving about together, one of the group gives a sharp *wak* or *wak-wak.* This call seems to be a mild signal alerting the birds, but its function and motivation are not obvious. Sometimes, one gives a low, harsh form of the *wak* call, usually in a monosyllable, and again, in social contexts that are not clear.

When truly alarmed, fruit-crows call with a considerably louder and more arresting version of the harsh *wak-wak,* usually of several syllables. They gave this alarm when flying predators appeared and also when one of our party climbed the nest tree and attempted to look into the nest. Later, I shall describe their mobbing behavior, a most important part of their nesting strategy.

If we allow for the subjective element in transcribing bird calls, it seems clear from the accounts of Chapman (1929) and Slud (1964) that the calls are essentially the same in Central America as in Guyana.

We saw one of the courtship displays of the fruit-crows when Male A began to try to entice Female A away from the nest which she was building, to a new nest site which he had chosen. He followed her persistently in short flights among the treetops, calling repeatedly, spreading his throat-fan widely, and shivering his tail. Later when showing the female the new site that he had chosen, he behaved in the same way. The only copulation we saw occurred on a different occasion, almost certainly involved other birds, and was preceded by no special ceremony.

Breeding

The Nest and Nest-building

The first nest, found by my wife near camp on 19 January, was 35 feet up, very near the top of a slender tree beside a forest trail. The main structure was complete but the lining was unfinished. The nest, a rather loose cup, consisted partly of twigs and partly of dry panicles of a vine (*Sparattanthelium wonotoboense*) which hung down in sprays from the top of a neighboring tree. These had been incorporated into the nest in such a way that the seed-heads themselves hung down in a fringe around the bottom of the nest. The fork, from which several fine branches grew obliquely upward, afforded good support for the apparently rather weak nest structure.

On 19 January, I saw Female A take a fine twig to the nest, place it in the cup, and then sit in the nest, shaping it with feet and breast and pulling in odd strands of material that were projecting from the nest rim. One of the males was perched about 18 inches away and, when the female left the nest he, too, went onto it and stayed for about 30 seconds, performing nest-shaping movements.

Nest-building continued intermittently for 26 days. Only the female brought material, but one male, almost certainly Male A, was seen to sit on the nest and shape it several times between 20 and 28 January as he had on 19 January. One time he stayed for four minutes. I never saw him bring material to the nest, but once he picked a twig from a tree near the nest and dropped it. Once Male B also picked and dropped a piece of the fruiting vine that was such a conspicuous part of the nest structure. I never saw Male B on the nest, but he often perched near it, and I never saw Female B do any building, but once she pecked at the material hanging below the nest and then perched just above the nest, looking down into it while Female A, which had just returned with nest material, waited on a perch nearby. I saw no aggression between any of the members of the group at the nest; on every occasion, if one was there first, the other simply waited quietly not far away.

These observations differ slightly from the reports of Ellis (1952) and Haverschmidt (1968). At the nest watched by Ellis the male brought material and the female did the building. Ellis did not describe the details of this cooperation. Haverschmidt briefly mentioned a male building a nest, without giving further details. All the observations agree, however, in showing that the male is actively concerned in the building of the nest and that he also plays an active part in the selection of the nest site. The exact role played by the male in the construction of the nest may well be variable. Also, since we did not see the construction of the main structure, it may be that, in the group we observed, the male built or helped build it, leaving the female to do the lining.

Most of the material brought to the nest for the lining consisted of fine terminal twigs of an abundant understory tree (*Rinorea brevipes*), the very fine twigs of another abundant small tree (Myrtaceae sp.), and once the fruiting panicles of the vine *Sparattanthelium wonotoboense,* already mentioned. The twigs of the myrtaceous tree were the main material used in the nest lining. They are very fine, tough, and springy, and branch obliquely at short intervals. They were also used in the lining of the second nest.

Between 19 and 28 January, I saw the female spend eight periods, of up to six minutes each, sitting on the nest, at times performing shaping movements but for much of the time sitting quietly. Then, on 29 January, she sat on the nest for 45 minutes during midmorning. On 30 January, she was on the nest in the morning for only nine minutes in a period of two hours and 40 minutes, and in the afternoon was not seen on the nest at all. On 31 January, she failed to appear at the nest in the early part of the day, but at 16:00 I saw her leave the nest and by 17:55 she reappeared and remained on the nest all night. On the following morning at 06:40 she left to join the three other birds as they flew, calling, to the nest from up the hill where they apparently roosted. I was surprised to find, on inspection, that the nest contained no egg.

From 31 January until 4 February, the female seemed to show little interest in the nest. From 4 to 9 February, she spent long periods visiting other possible nest sites, concentrating, from 5 February, on a high branch of a huge Mora tree (*Mora excelsa*) in the camp clearing. One of the males — probably Male A, although I could not distinguish the two at this time — always took the initiative, flying to the Mora branch and calling from there. The female followed, alighting on one particular fork where she sat, calling and making settling movements. It appeared that the male was "dissatisfied" with the original nest site; but none of the Mora forks looked as substantial to us as the fork already containing the nest. Possibly the Mora site, about 75 feet up, was nearer the height preferred by fruit-crows for their nests. Our second nest, and the two reported by Ellis and Haverschmidt, were all between 65 and 75 feet.

The female continued, however, to visit her nest occasionally during the period when she inspected the Mora site. After 9 February, we did not see her again at the Mora site. On 6, 8, and 9 February, I saw the female spend four periods, each of about two minutes, on the nest. On 9 February, she began taking nest material to it again after an interval of 11 days, and she continued to do so until 14 February. On 16 February, after spending little time at the nest for two days, I found her sitting in it in the late afternoon, and she remained on it for the night. I inspected the nest when she left at 07:00 the following morning and found an egg. It was visible through the bottom of the nest cup, which, after four weeks of desultory lining, still let through chinks of light.

Throughout the nest-building period all four birds regularly came and went from the nest as a group. Typically, Female A led, followed closely by

Males A and B, with Female B straggling in the rear. They swooped in, Female A and Male A and often Male B landing in the nest tree while Female B perched in a tree nearby. Female A first went to the nest, and after she had finished building and had flown to a perch in an adjacent tree, Male A often went and perched on the nest edge, looking down into the cup for a few seconds. Sometimes, during the early days of observation, he sat in it and carried out nest-shaping movements. When they all flew off, Male A was in the lead.

The fruit-crows made no attempt to conceal the position of the nest, which in any case was fairly conspicuous as the tree had very thin foliage. Both male and female called when perched at the nest with normal loudness, vibrating the tail conspicuously. At times, three fruit-crows perched within a few feet of the nest. Observation was unusually easy for us, apart from the fact that the nest itself was inaccessible, as at no stage in the nesting cycle did the birds pay the slightest attention to a person standing just below the nest, only about 30 feet away.

Our observations at the second nest were far less complete. This nest we found by following the group when they were building. We had seen two females collecting twigs from a tree — the same myrtaceous species which was used for the lining of the first nest — about 100 yards from their nest site. We saw only one female, however, go to the nest with material, and it seemed probable that the other was picking material and dropping it, just as Male B and Female B did at the first nest. The male regularly went onto the nest and on one occasion sat for two minutes while the female waited on a perch just below.

The second nest was about 70 feet up in a tree about 100 feet high, on sloping ground in forest where there was no closed canopy but a rather open growth of large, but mainly slender, trees. Although similar to the first nest, it appeared a little more twiggy, perhaps because it lacked the fragments of fruiting vine that hung down from the other nest. It was placed in the same kind of fork and was clearly visible from below, but not with comfort, since a thick understory of vegetation hid it except from one position almost directly below.

The fruit-crows at the second nest behaved very like those in the first group. All three flew to the nest tree together, calling, and making no attempt to make themselves or the nest inconspicuous.

Defense of the Nest

Neither the location of the nests, nor the behavior of the nesting adults at either of the nests, suggested that in this species it can be at all important for the safety of the nest that it should be inconspicuous, as are so many nests in tropical forest; but it is certainly significant that both nest trees, along the entire length, were growing clear of other trees. Once a group of Capuchin monkeys (*Cebus capucinus*) passed close to the camp nest, and once a troupe of squirrel monkeys (*Saimiri sciureus*) passed through trees adjacent to the other nest. In neither case did the monkeys climb the nest tree, which they could not have reached without first descending to the ground. The choice of nest trees that are clear of the surrounding vegetation may be an important adaptation in tropical forest, as suggested also for the Bearded Bellbird (*Procnias averano*) by Snow (1970).

It soon became clear that the fruit-crows' method of ensuring the safety of the nest against avian predators is to establish a zone around it in which they are dominant and from which they persistently chase most other birds. The fruit-crows regularly mobbed intruders near the nest during nest-building and on through the breeding cycle until our observations ceased, shortly before the one young flew. On some days, mobbing took up a considerable part of their time.

Slud (1964) recorded that he had seen fruit-crows make passes at a perched hawk and mentions that they are also apt to worry a large toucan; but he commented that the fruit-crow's "limited powers of flight might make it an easy prey for a raptorial bird." Actually, fruit-crows are extremely agile on the wing, and it seems likely that this agility may be related primarily to its mobbing of nest predators rather than to its methods of feeding, because birds with far weaker powers of flight, such as trogons, feed in essentially the same way as the fruit-crows. Similarly, the black plumage may result from the positive selection for a conspicuous, "aggressive" color. The black of such aggressive birds as drongos (Dicruridae) may have the same explanation.

Fruit-crows occasionally mobbed toucans at distances up to 200 yards from the nest, but mostly they mobbed birds that came within about 50 yards of the nest. The members of the camp group spent much of their time within 100 yards of the nest. They returned to its vicinity at intervals after they had fed farther afield, resting and preening usually on high perches within sight of the nest. Thus, it is improbable that a potential predator would usually have been able to approach the nest without being detected. However, there were periods, of not more than a few minutes, when all the birds were well away from the nest, and its safety seemed to be left to chance.

When mobbing an intruder, fruit-crows utter the *oo-waa* call repeatedly, occasionally varying it with the drawn-out, upwardly inflected *oooo*. They face the intruder, lower the head, and while calling fan out the throat-ruff and shiver the tail. Sometimes they snap the beak several times in quick succession. If the intruder is in an accessible position, they dive at it repeatedly, one after the other, coming to within a few inches of it and then swerving away at great speed. At the closest point, they utter a curious rasping call never heard on other occasions.

An intruding bird may enjoy a degree of immunity if it perches quietly in thick cover where the fruit-crows cannot dive at it. As soon as it flies, however, they are after it at once, often in a close pack, pursuing it closely and harrying it until it is well away from the nest area. Once, what appeared to be a tail feather fluttered from a jay that the fruit-crows were pursuing in this way. If there are several intruders, the fruit-crows may split their forces, paying most attention to the birds closest to the nest.

A few observations showed that instead of mobbing flying predators, and perhaps particularly dangerous climbing predators, fruit-crows utter alarm calls and get out of the way. On two occasions when a hawk — probably a *Micrastur* sp. — flew over a nest, the fruit-crows uttered a sharp *wak-wak-wak* and dived down to lower perches; and once they called in the same way when a Turkey Vulture (*Cathartes aura*) flew overhead. When our Indian helper attemped to climb to the camp nest with a mirror mounted on a rod, the birds gave the same call, and they repeated it later when I approached the nest. Some birds other than fruit-crows may interpret this call as a warning. On more than one occasion, when the fruit-crows uttered it near a Capuchinbird (*Perissocephalus tricolor*) display ground, the Capuchinbirds at once dived down from their display perches into lower cover.

Altogether, we saw the fruit-crows at the camp nest mob 13 species of birds. Toucans (*Ramphastos vitellinus* and *R. tucanus*) and Cayenne Jays (*Cyanocorax cayanus*) were the species most frequently mobbed, accounting respectively, for nine and eight of the 33 mobbings recorded. Fruit-crows also mobbed the Green Toucan (*Pteroglossus viridis*); three hawks — a species of *Buteogallus*, Black-faced Hawk (*Leucopternis melanops*), and one unidentified; three icterids — Crested Oropendola (*Ostinops decumanus*), Yellow-rumped Cacique (*Cacicus cela*), and Red-rumped Cacique (*C. haemorrhous*); the White-tailed Trogon (*Trogon viridis*); the Black-tailed Tityra (*Tityra cayana*); the Guianan Cock-of-the-Rock (*Rupicola rupicola*); and a small flycatcher; and once a troupe of monkeys. Those birds that were not potential nest predators were mobbed rather half-heartedly or even ignored, unless they happened to come very close to the nest, in which case they were driven away vigorously.

Mobbing nearly always succeeded in causing the intruder to leave the nest area, except in the case of the Black-faced Hawk. This bird, certainly the same individual on the four occasions recorded, stolidly perched in a tree near the nest, taking little notice of the succession of diving fruit-crows that passed within inches of its head and only occasionally raising a foot to ward them off. Twice this hawk distracted the fruit-crows for so long during my watches at the nest that I eventually drove it off myself. Whether it actually had designs on the nest, I never knew.

At the camp nest, intruders became less frequent as the nesting cycle continued, presumably because they learned to avoid the constant harrying to which they were subjected in the area. I recorded 12 mobbing incidents in 19 hours and 20 minutes of observation during the nest-building period; 10 in 37 hours and 20 minutes during the incubation period; and only five in 28 hours and 20 minutes during the nestling period—a decline from one incident about every 40 minutes to one about every six hours.

Incubation

Female A in the group at the camp nest laid the only egg in the clutch early on the morning of 17 February. She left the nest at 07:00 hours in response to the calling of the others near by. Fifteen minutes later, they all returned to the nest. The two males perched near the nest and both looked down into it; twice one of them moved closer and the other displaced it. Female B, meanwhile, was on a higher perch in a neighboring tree, well above the level of the nest, and must have been able to see its contents. At 07:16, Female A went to the nest and settled down on it. Thus, within a short time of the laying of the egg, all members of the group had almost certainly seen it.

The routine of incubation remained much the same throughout the period. Only Female A incubated. Between the times when she first left the nest in the morning (between 06:50 and 07:12 for seven records) and the time she finally returned to it and stayed for the night (once at 16:35, and from 17:18 to 17:47 on five other occasions) she sat for about two-thirds of the time. Thus, in one complete day's watch she sat on the nest 67 per cent of the time; in the six shorter watches, totaling 14 hours, she sat 62 per cent of the time.

The female's absences from the nest were much less variable in length of time than her sessions on the nest; exactly half of the 50 recorded absences were from 12 to 17 minutes. Only two absences were longer than 23 minutes, 26 and 31, and only one was less than six minutes — a four-minute absence caused by the female leaving the nest prematurely on an alarm and soon returning. By contrast, her sessions on the nest varied from half a minute to one hour and 15 minutes, with the majority toward the lower end of this range. I recorded only four sessions on the nest of more than 50 minutes, but there was some bias against the longer sessions because we could record them only during long watches.

Early in the incubation period, the female's departures from the nest were usually stimulated by the other fruit-crows in the group. After a period of perching quietly near the nest, they grew restless, began to call, and then flew off to feed, whereupon Female A left the nest and joined them. Later, her departures seemed more often spontaneous in that she left when the others were silent or out of sight. Several times she left the nest to join the others in mobbing an intruder. Such instances account for several of the very short sessions that we recorded.

Just as during nest-building, all four fruit-crows normally returned to the nest together with Male A leading. Often Male A flew into the nest tree accompanied by the female and sometimes by Male B too. Much more rarely, Female B joined them in the nest tree. Male A sometimes went to the nest and perched at it for a short time while Female A waited on a lower perch; he then flew to a lower perch or out of the tree altogether and Female A at once went onto the nest. Sometimes the female alone flew into the nest tree and all the others landed in a tree near by; and rarely, the female returned to the nest alone, although on such occasions the other birds were not far away.

Throughout the incubation period, we could see the egg against the sky through the bottom of the nest cup. Attempts to view the egg directly from above by climbing adjacent trees, or by holding up a mirror fixed to a long pole, were unsuccessful; the tree was too slender to be climbed. From 8 March, when the egg had been incubated for 19 days, I checked it regularly from below.

The first sign of hatching occurred on the afternoon of 11 March, when the female appeared very restless. She left the nest and returned to it at short intervals, and at times stood looking down into it and turning her head sideways. Later events suggested that the female was probably beginning to hear the chick call inside the shell. On 12 and 13 March, the female was more settled and the egg was still visible in the nest. Then on 14 March, after 25 days of incubation, I found half of the eggshell beneath the nest. It was exceedingly dark with a deep olive ground color rather thickly covered with blackish-brown markings.

The second nest apparently failed soon after the egg was laid. On 28 February, 11 days after we found the nest, the female was sitting on it. In the course of a three-hour watch in the morning, she sat for periods of 12, 31, and 65 minutes, and left for periods of 9, 8, and 11 minutes. When leaving and returning to the nest, she was accompanied by the other birds of the group. For the first 57 minutes of the watch, however, the nest was unattended and it seemed likely that she was just beginning incubation; indeed, she may have laid the egg that morning. On subsequent visits to this nest, on 3 March and several days later, I saw no birds either at it or near it. The nest appeared undamaged though it was far too high to be examined properly. This group of fruit-crows apparently began to build elsewhere; later, one of the females was seen collecting nest material, but the nest was not found.

The Nestling Period

The female was still on the nest at 06:45 on the morning the egg hatched, and half of the shell was lying on the ground below. At 07:07 she left the nest for 10 minutes, during which time the two males successively perched at the nest and looked in. One male seemed to be trying to feed the chick though nothing was visible in his beak. On this day, the female spent the greater part of the morning brooding the chick. Thus she was on for 95 per cent of a watch of just over two and one-half hours in the early morning, and for 88 per cent of one hour at the end of the morning; but she brooded the chick for only 38 per cent of an hour in the late afternoon.

On this day, one of the males, and perhaps the other, offered food to the chick three times during the four and one-half hours of observation; several times the female stood up in the nest and held her head low in the nest for a few seconds, apparently offering food. The food items were all small. Once a tiny insect was seen in the tip of the male's bill; on other occasions the bird moved his bill as though shifting food forward inside but nothing was visible.

Over the next three weeks, the female spent increasingly less time at the nest. Morning watches of two hours or more, when the chick was age 2, 6, 9, 12, 14, 17, and 21 days, gave the following percentages of time on the nest: 77, 60, 30, 18, 16, 9, 3. She regularly attended the nest less in the afternoon, but we watched less at that time. We never watched in the early afternoon during the only period that the nest was exposed to the hot sun. She may have shielded the nestling at that time; clearly she had felt the heat when incubating at that time of day. After the chick was a few days old, it was regularly left uncovered during light or moderate rain.

All four adults brought food to the nest, but in unequal amounts. During the first few days of the nestling period, it was difficult to be certain of the relative contributions of each bird; the two males were not distinguishable until the chick was six days old, when Male B lost his central tail feather; and when the female lowered her head in the nest, as she did at intervals when brooding, it was not possible to tell whether she was feeding the chick or tending it in some other way. By the third day, however, it became clear that the female was providing only a small part of the food. From 20 March, when the chick was six days old, until we left on 4 April, I recorded 78 visits with food by the two males and 16 by the female. I saw Female B go to the nest with food only once. In the course of the watches when a special effort was made to distinguish the males at all their visits to the nest, Male A made 36 visits and Male B 13 visits. Unfortunately, to distinguish between the two males, I had to stand directly below the nest in a position that was not always suitable for watching other activities.

During the nestling period, the adults usually maintained the following routine. Just as the male flew in with food, the female left the nest. Usually, he alighted on a perch just below the nest and, after a few seconds, flew up to the nest and perched on it. As during incubation, the three other birds of the group normally approached the nest together; the other male perched either in the nest tree or in an adjacent tree while Female B perched a little farther away. When the first male (usually Male A) left the nest, Male B, if he had food as he did on a small number of occasions, flew to the nest, delivered it, and then all four birds flew off together, Male A leading and Female B in the rear. One or both of the males sometimes returned again with food while the female was still on the nest. Then, after a few minutes, the female returned perhaps fed the young herself, and settled down to brood again.

Later, when the female was brooding less, her departures were more often spontaneous; but the group continued to approach and to leave the immediate area of the nest in a body.

The young bird was fed almost entirely on insects. I could not recognize the smaller items brought in the first few days; by the fourth day small katydids were being brought. From day 6 to 21, the food consisted of katydids, moths, cicadas, and mantids, together with many other adult, winged insects and small numbers of insect larvae. All the large insects were held with the head pointing forward and the wings, and sometimes the legs, sticking out to the sides. On day 12, an adult brought a fruit to the young, and over the next nine days I saw them bring three more fruits, one of which was probably from a Matchwood tree about 100 yards from the nest. Thus, of 76 feedings which were recognizable, only four consisted of fruit. The female fed regularly on fruits at this time, the seeds of which we collected in a sheet slung beneath the nest. Throughout the 21-day period of observation, the adults swallowed the fecal sacs which the chick produced immediately, but not every time, after feeding.

During morning watches of two hours or more, the adults fed the young at the rate of two to seven times each hour, and exactly four times an hour during the longest watch of six hours, from 06:30 to 12:30. Feedings tended to be clumped so that the shorter watches gave widely varying averages.

Although three of the adults regularly fed the young bird, Male A alone contributed 60 per cent of all the food, and he evidently had no difficulty in increasing his rate. He regularly brought food to the nest at short intervals, especially in the early morning. On four occasions, he fed the chick three times in 13 minutes or less. Once he fed it three times in eight and one-half minutes and once, three times in nine minutes. On one occasion, in the late morning, he fed it four times in 16 minutes; and once, after feeding had been interrupted for about an hour while the adults mobbed a hawk near the nest, he brought food four times in 27 minutes. The adults regularly offered the nestling more than it could take. It refused the food offered on 10 out of 95 occasions on days 6 to 21; earlier, when it was two days old, it refused three of 11 offerings of food.

The nestling was covered in buff-colored down, which by day 12 appeared speckled with black from the feathers growing beneath it. When the nestling was 17 days old, it still appeared buffy with black patches, and the flight and tail feathers seemed to be about one-third grown. The long quills, terminating in the expanded black vanes, gave the wings and tail the appearance of a Chinese fan. At the age of 20 days, the head and the wing coverts appeared black with scattered buffy spots. My observations ceased when the nestling was 21 days old, but Mr. William Clements, our camp helper, visited the nest regularly until the young bird left when it was 32 or 33 days old.

Discussion

The Purple-throated Fruit-crow's breeding strategy seems to be founded on active defense of the nest; and this must have favored the evolution of communal groups with an extreme reduction of intraspecific aggression. None of the other cotingids, whose habits are known, has a comparable system. The Red-ruffed Fruit-crow (*Pyroderus scutatus*), also the single representative of its genus, is closest to *Querula* in general appearance though considerably larger; but the very incomplete accounts of its behavior suggest that the males display communally (Olalla, 1943), and may also hold individual territories (Hamilton, 1871). They have a booming call, and the difference in size between the male and female is much greater than in the Purple-throated Fruit-crows. On the other hand, T. K. Salmon (quoted by Sclater and Salvin, 1879) reported that it defends its nest fiercely against hawks. A thorough investigation of the ecology and behavior of *Pyroderus* would be of the greatest interest.

I suggested earlier that the peculiarities of the fruit-crow's wings and tail, which for a cotingid are unusually ample and make the bird highly maneuverable in flight, are primarily adapted to its mobbing behavior rather than to its method of feeding, and that the black plumage may also be advantageous in that it is conspicuous and intimidating. The bird's behavior and nest site compensate for the lack of a cryptic plumage. These factors may also account for the absence of juvenal plumage. The Bare-necked Fruit-crow (*Gymnoderus foetidus*), another large, mainly black cotingid, has a highly cryptic nest (Béraut, 1970) and a very distinct vermiculated juvenal plumage.

If the history of a single nest kept under detailed observation is typical, the single-egg clutch is remarkable. In this case, it seems unlikely that the amount of food that the adults were able to supply could possibly have limited the clutch size to one. Four adults were available to feed the nestling and all brought food, but in fact one male did most of the feeding, and the chick was regularly offered more than it could eat. As pointed out by Snow (1970), all the larger cotingids that build open tree nests, as far as we know, lay only one egg. With *Querula* now added to the list, it seems that we must seek some more general explanation for the small size of the clutch, an explanation unconnected with the feeding ecology of any particular species.

The fruit-crow's incubation and fledging periods are, for its size, very long. Both are almost the same as those of the distinctly larger Bearded Bellbird, which has a notably slow development (Snow, 1970). As the young fruit-crow's diet consisted almost entirely of insects, we may have to reconsider the suggestion that the bellbird's long fledging period is adapted to a fruit diet, poor in protein. Lack (1968) gave few details for the Cotingidae, and a thorough discussion of the rates of development in this family must still await the accumulation of more field data.

Summary

This paper is based on a study of the Purple-throated Fruit-crow (*Querula purpurata*) from January to April 1970, in the foothills of the Kanuku Mountains in southern Guyana, where they live in small communal groups of from three to four birds, with strong social bonds and an almost complete absence of aggressiveness between members of the group.

The adults feed partly on insects and partly on tree fruits, both usually taken on the wing. The fruits of four trees (*Didymopanax morototoni, Hirtella* sp., *Guarea trichiliodes,* Lauraceae sp.) were especially important during the period of observation.

We found two nests, one of which was successful. Both nests consisted of open cups made of sticks and were situated in isolated trees. The birds made no attempt to conceal the nest, which they defended vigorously by mobbing intruders at all stages of the nesting cycle.

The clutch in the one successful nest consisted of a single egg. Only the female that laid the egg incubated it, but all four members of the group brought food to the young. The incubation period lasted 25 days.

The members of the group fed the nestling almost entirely on insects and regularly brought more food than it could eat. One male did 60 per cent of the feeding and he apparently had no difficulty in increasing his feeding rate as the occasion demanded. The young bird left the nest at the age of 32 or 33 days.

We suggest that the fruit-crow's breeding strategy has been an important factor determining its body proportions and its social behavior. The one-egg clutch cannot be an adaptation to the number of young that the adults can feed. We need more information on other species of Cotingidae before we can discuss thoroughly the very long incubation and fledging periods of this and other members of the family.

Acknowledgments

I am very grateful to my wife for help with the observations. She first saw the nest near our camp and, while watching the display ground of Capuchinbirds, saw fruit-crows collecting nest material, which led to the discovery of the second nest. She also helped in the day-long watch at the camp nest. Mr. William Clements, our helper, continued to visit the camp nest after we left, and Mr. Carl Hopkins of Rockefeller University, who was in a camp nearby, very kindly supervised his visits. Dr. R. M. Harley of the Royal Botanic Gardens, Kew, kindly identified plant specimens.

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Verreaux's Eagle, *Aquila verreauxi*. Drawing by Tony Angell.

THE LAYSAN ALBATROSS: ITS INCUBATION, HATCHING, AND ASSOCIATED BEHAVIORS

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Photographs by the author

The Laysan Albatross (*Diomedea immutabilis*) nests in colonies on the atolls in the North Pacific. In recent years, its confrontations with the United States Navy over the problem of land usage on Midway Atoll have made newspaper headlines and aroused conservationists. The birds nested, or tried to nest, where they always had; they flew in and out of their colonies as usual, disregarding the macadam roads, cement runways, buildings, and networks of wires in the Navy installations, and apparently unmoved by lumbering trucks and flying planes. Many birds died in collisions with cars, planes, and wires; a few Navy planes were damaged and Navy nerves were frayed. Neither side won, but when the Navy discontinued the early warning DEW Line and the largest antennas were taken down, life for the albatrosses on Midway became less hazardous.

One purpose of my research of the biology of the Laysan Albatross (Figure 1) was to determine the behavior of the incubating birds, their success in reproduction, and the rates and reasons for the loss of nests and eggs. I also examined in detail the data on the length of the incubation period and the participation in nesting by members of the pair. Although Hadden (1941), Sheehan (1952), and Rice and Kenyon (1962a,b) reported on these aspects of the life cycle of this albatross, certain phases needed verification and amplification.

Research in the breeding colonies extended from 1961 through 1969. We collected the bulk of the data from 1961 to 1967: during the egg-laying period in each of the nine years, the incubation period in 1962–1963 and 1968–1969, and through the entire breeding cycle in 1964–1965.

Most of our data came from a permanent research plot (hereafter referred to as the colony) on Eastern Island of Midway Atoll, but some from intermittent observations on Sand Island of Midway and on Kure Atoll about 52 miles northwest.

Methods

Chandler S. Robbins, Dale W. Rice, Karl W. Kenyon, my assistants, and I banded more than 99 per cent of the breeding birds in the permanent research plot — chicks only in 1956 and 1957, chicks from 1961 through 1963, and in 1965 and 1969. After we banded the first breeding birds in 1960, we banded all birds found breeding each year. Consequently, we know the exact age, within a month, of many of the albatrosses in the plot. And now, even if we do not know a

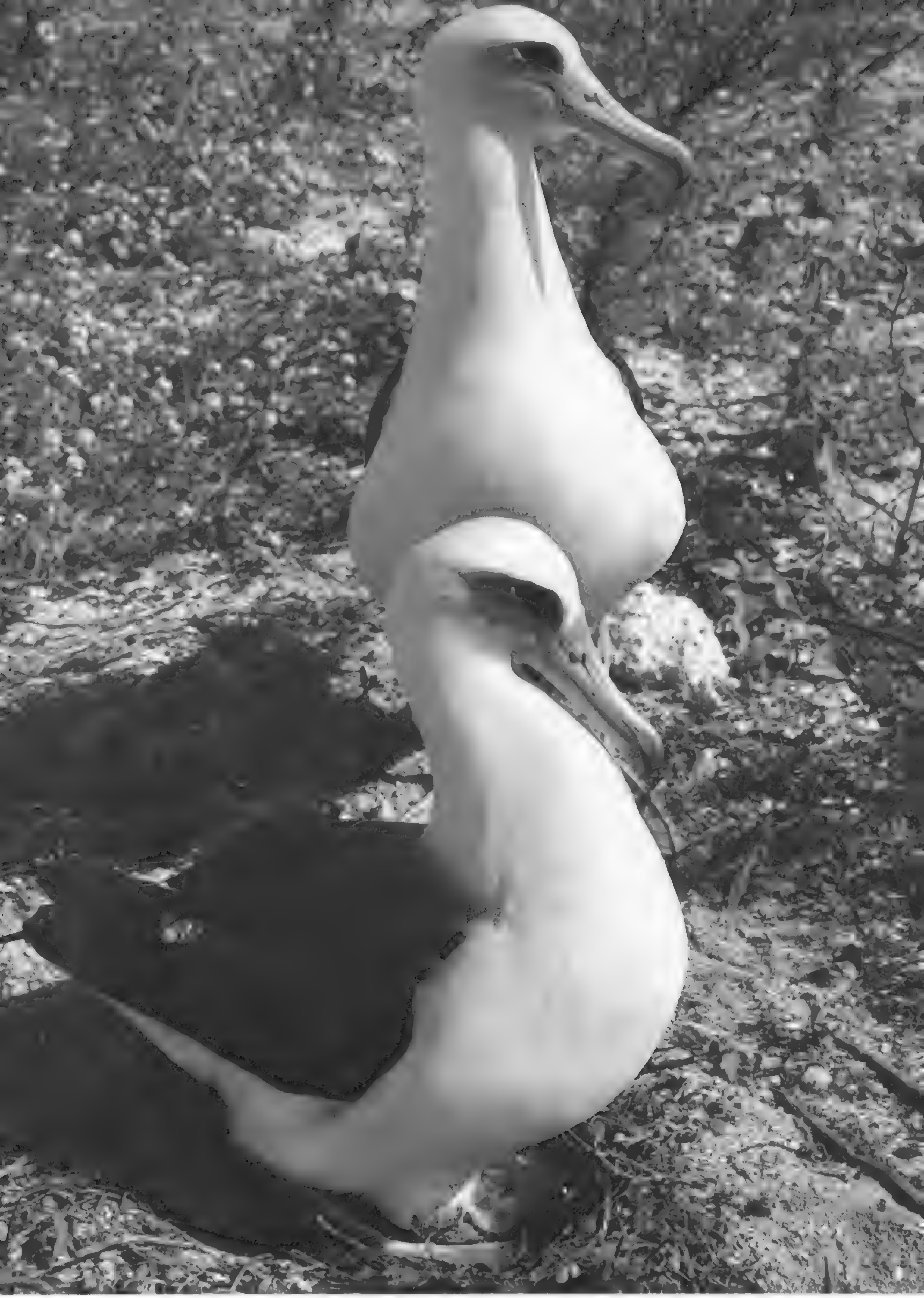


Figure 1. A pair of Laysan Albatrosses at the nest; the female is on the egg.

bird's age, we can tell from our records whether it has bred previously (experienced) or is breeding for the first time (inexperienced).

We have information on more than 5,300 incubating pairs, but in this study emphasis is on detailed data on 620 nests in 1962-1963, 350 in 1964-1965, and 476 in 1968-1969, seasons when we checked every nest, bird, and egg every morning from the time the first egg was laid until the last chick hatched. With observations 24 hours apart we may have a one-day error in the lengths of the incubation period and of the individual spans. The large number of nests in our sample reduces this error considerably, if not entirely.

We identified each nest by placing a numbered stake one foot north of its edge. Because the nests were close together and because an incubating albatross tries to cover any egg it sees, we had to be careful, when lifting a bird from its nest for examination and thus exposing its egg, that a neighboring bird did not move over and sit on the egg. Such instances apparently occurred in previous studies and confused the information on pair-bond and nest-relief. To prevent further errors, we carefully returned each bird to its own nest and waited to see that it stayed there.

After examining the albatross, we placed it on the ground, belly down with its bill on the edge of the nest, and scratched the back of its head gently until it relaxed. Within a minute or so, in most instances, the bird jumped up, shook itself, and moved onto its egg. If we scratched too long, or the bird was unusually sensitive, it sometimes relaxed flat on the ground (Figure 2) for as many as five minutes. During this interval, birds on nearby nests or birds walking past often tried to sit on the uncovered egg. Consequently, we always watched until we were sure the owner was incubating.

Some birds relaxed and recovered quickly, jumped up and onto the nest; infrequently, a bird that did not relax at all left the site. We recorded all the departures and subsequent mix-ups with pairs on adjacent nests, but we have not included the data in the summaries on the length of the incubation spans or the total incubation time.

The physical identification of the sex of an albatross is reliable only during the copulation and egg-laying periods of the pair — no more than 10 to 15 days. We determined the sex by cloacal examination each year and verified it from records of the make-up of the pair in former and later years. We marked males on the crown of the head with red paint and females with black or deep blue so that we could study the duration of attentive periods, exchanges at the nest, and other behaviors without disturbing the albatrosses.

Incubation Pouch

Both sexes of currently breeding birds develop an incubation pouch. The loss of down feathers from the midline of the adominal apterium just behind the sternum leaves a cavity, averaging 50 by 95 millimeters, covered by the stiff contour feathers of the abdomen. Because of its sac-like nature

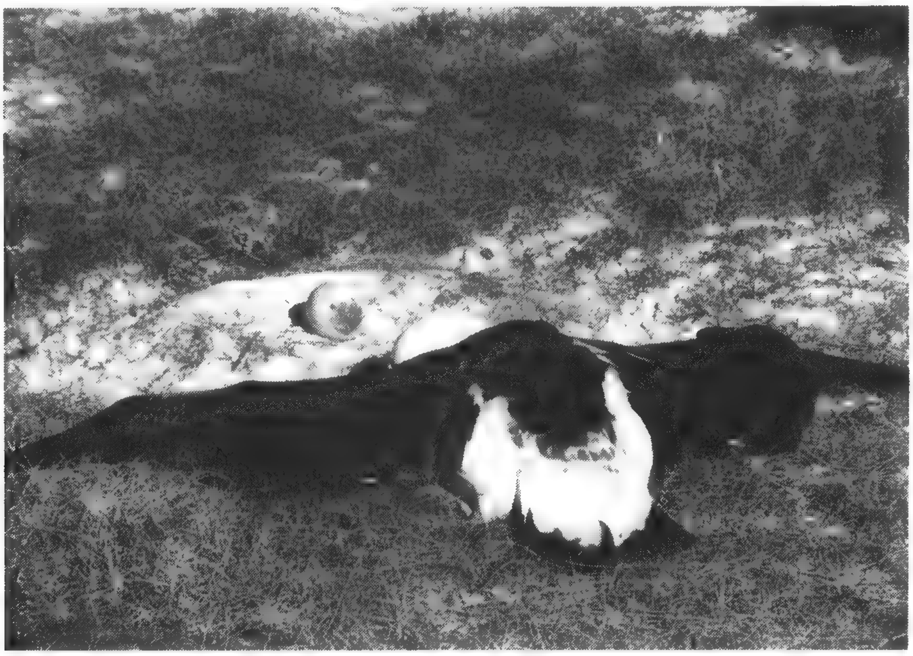


Figure 2. This breeding Laysan Albatross stretches out on the ground in a "relaxed state." After lifting the incubating bird and examining a nest, we initiated this condition by gently stroking the back of its head. The relaxed bird soon recovered and moved onto its egg.

we call the cavity a "pouch" rather than a "patch" (Figure 3). The blood vessels in the thickening skin of the pouch increase and enlarge beginning with the first loss of down and usually persist until most of the down is replaced.

The pouch accommodates only one egg that fits so tightly that it frequently remains within when the bird stands (Moseley, 1879:172; H. I. Fisher, 1968). The similarity of the temperatures of the skin and egg, 36.7°C and 36°C respectively, proves that the pouch is a well insulated container (Howell and Bartholomew, 1961a:187).

Although the pouch begins to develop in some experienced birds before they return to the colony, it is seldom complete on arrival. All experienced birds that are to breed that season have a completed pouch before egg-laying begins on 20 November. This contrasts with the Madeiran Storm Petrel (*Oceanodroma castro*) which forms a pouch as long as 40 days before laying (Allen, 1962). Breeding male Laysans develop the pouch about a week earlier than breeding females. Birds breeding for the first time may not have a completed pouch before 1 December.

The refeathering of the pouch, first indicated by the blue shafts of incoming feathers, begins in mid-January in some incubating birds and is obvious by the first week of February in approximately 50 per cent of the birds that

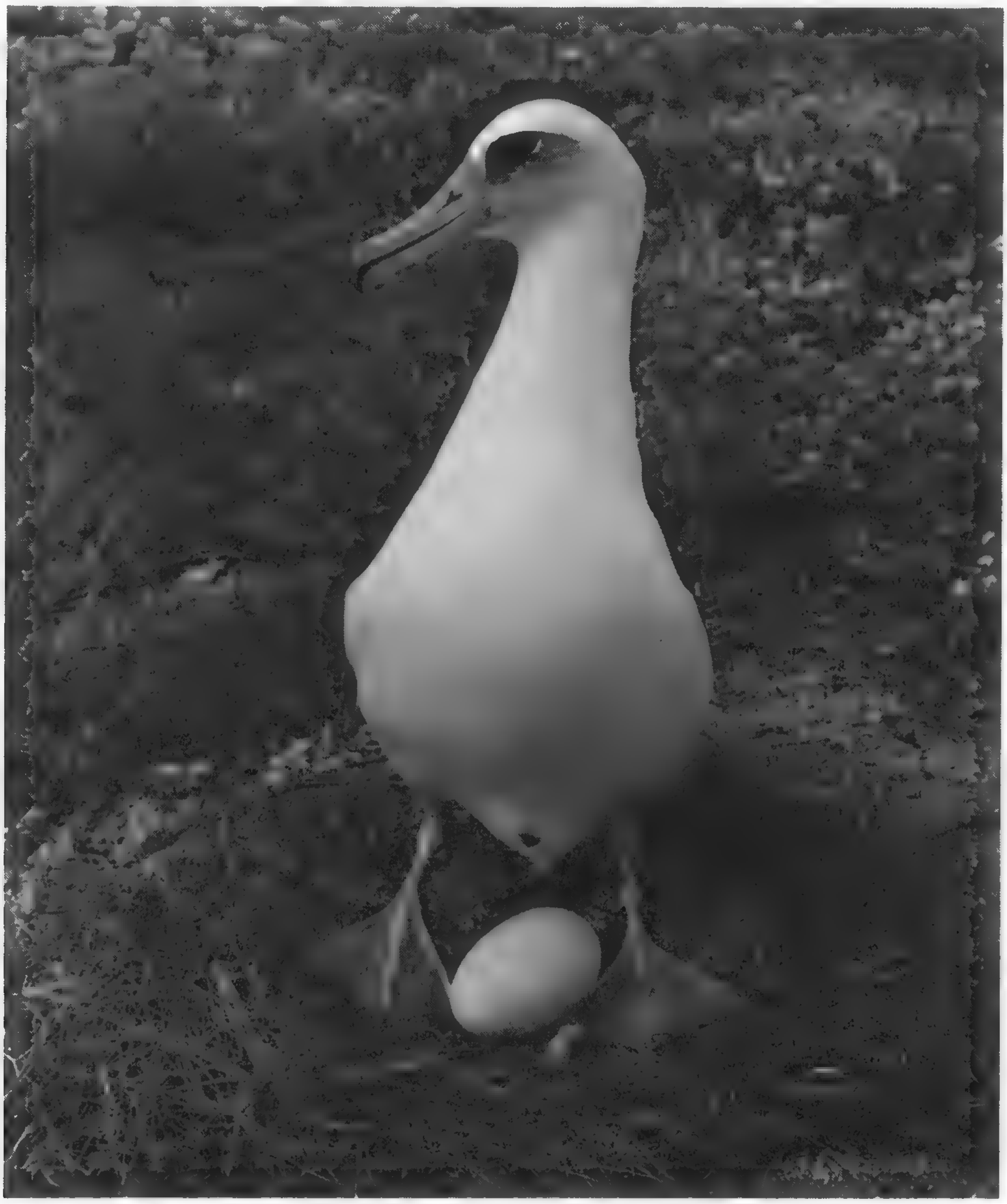


Figure 3. An incubating Laysan Albatross showing the egg that has just dropped from the incubation pouch.

are still on eggs or are brooding chicks. Most breeding birds have no pouch after 1 March. However, individuals vary. Old females, which lay on 27 November, may have a bare or completely feathered pouch by 1 February, as may their mates. Young pairs, which are nesting for the first time and lay eggs between 3 and 8 December, have pouches in the same condition as the old females by 1 February.

Birds that fail in their breeding attempts — if they have a pouch — follow the refeathering pattern of the successful breeders. In experienced birds, not currently nesting, 70 per cent of the males and 45 per cent of the females have a completely bare pouch. Early December body weights of 63 paired, former breeders — 32 males, 31 females — with no or only a slight sign of a pouch, were significantly less than the body weights of breeding birds; the males weighed 16 per cent less; the females 19 per cent less (H. I. Fisher, 1967). The degree of pouch development in these former breeders does not seem to be correlated with the bird's association with a mate. The refeathering in both sexes of these non-breeding birds is usually complete by 15 February.

Juveniles show a different chronology. None has a pouch when it first arrives in the colony. Seven- or eight-year-olds that may breed the following year often begin losing the down in the pouch area in mid-December and early January; one-third of these males and one-tenth of the females complete the pouch in December. During January, only one-fourth of these males and females have bare pouches; few retain them beyond February.

A December sample of 62 seven- and eight-year-olds, associating but not breeding, showed that in 57 per cent of the pairs both members had pouches in the same stage of development; in 32 per cent the male's pouch was more developed; in five per cent, the female's; and in six per cent, neither member had a pouch. A January sample of 19 similarly associating pairs showed that in 63 per cent the members were in the same stage; in 32 per cent the male was ahead; and in five per cent, the female. In all instances, when the female's pouch was more developed, she was associating with a male younger than herself.

In the six-year-olds, the maximum pouch development usually comes in late January or February, and refeathering occurs in March and early April. Some, but not all, of the four- and five-year-olds show some pouch development in late February, March, and early April. Unpaired males usually have more complete pouches than do young females. We found no pouches in birds less than four years old.

Length of the Incubation Period

Hadden (1941:34) reported first on the incubation period of the Laysan Albatross: ". . . 9 weeks for the egg to hatch . . . ." Sheehan (1952) defined the average length as 64.5 days. Rice and Kenyon (1962b:541–542) recorded a mean time of 64.4 days for 95 eggs, with a modal time of 64.0 days and a median time of 64.5 days.

Our data from 432 nests where the owners behaved normally — 256 in 1962–1963 and 176 in 1964–1965 — were: average incubation period, 65 days (55–72); modal, 65; and median, 64–65. Ninety-three per cent of the eggs hatched on or between Days 63 and 67; 77 per cent hatched on Days 64, 65, and 66.

In 1962–1963, the first season we gathered data throughout the incubation period, the range of incubation time and the eggs that hatched "early" and

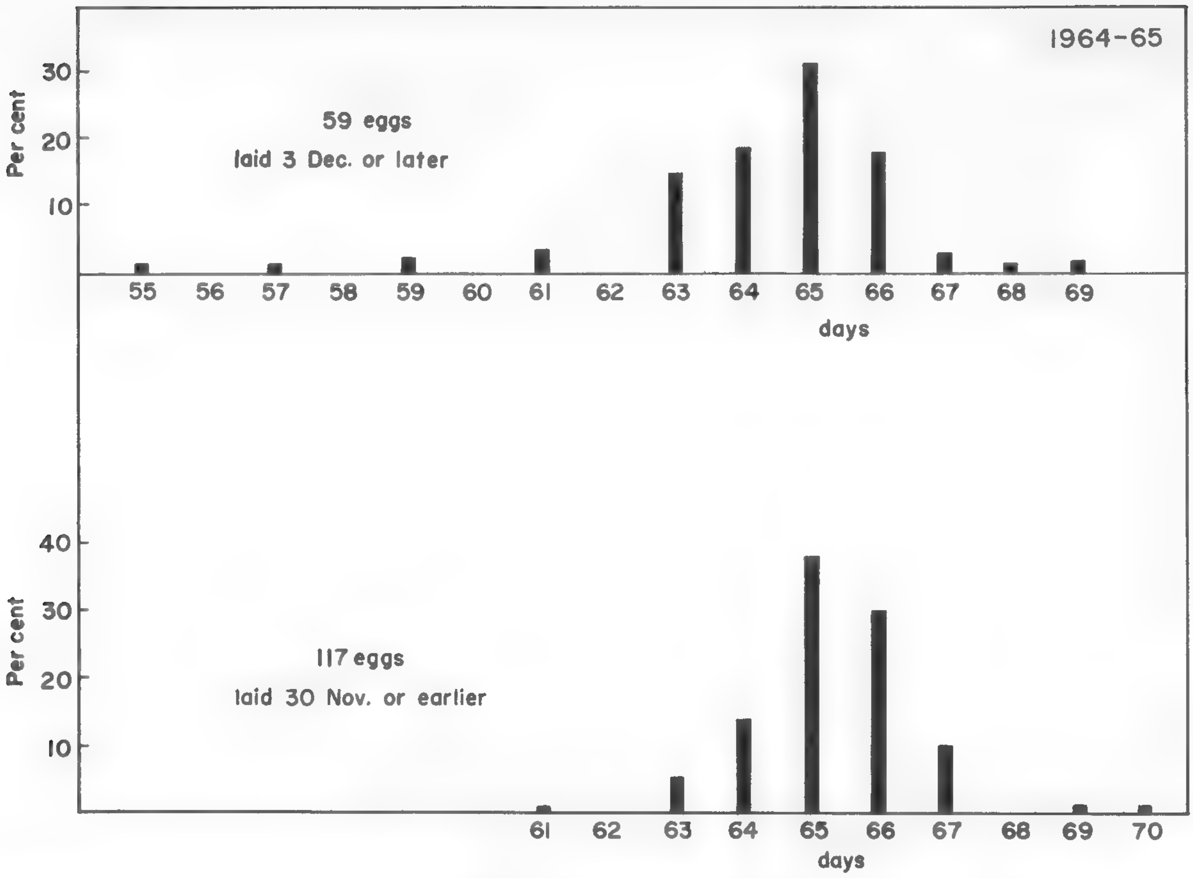


Figure 4. Comparison of incubation periods of eggs deposited early and late in the laying season. The average incubation period of the 59 eggs was 64.7 days; the 117 eggs, 65.4 days.

TABLE 1

Length in Days of Incubation Spans of Male and Female Laysan Albatrosses, 1962 and 1963

Span number	*Sex*	*Number of birds*	*Mean*	*Median*	*Mode*	*Range*
1	F	686*	2.1	<1	<1	0–32
	F	75	3.0	2	<2	0–32**
	F	593	1.7	<1	<1	0–14***
2	M	166	24.1	24	23	9–58
3	F	451	20.3	21	20	6–38
4	M	269	14.2	14	14	1–32
5	F	109	7.0	7	8	1–24
6	M	36	4.8	5	5	1–11
7	F	2	1.5	—	—	1–2

*Total is 18 birds greater because 18 mates were not determined.

**Eggs laid after 6 December.

***Eggs laid before 7 December.

"late" aroused our curiosity. On Days 55, 58, and 59, one egg hatched; Day 61, two; Day 62, 11; Day 69, three; and Day 72, one.

Further investigation of the pairs with eggs that hatched early and late led to a comparison of the length of the incubation period in old and young birds. In 1962–1963, all six eggs incubated for 67 days or more were laid before 2 December by experienced females; all 16 eggs incubated for 62 days or less were laid after 2 December by birds breeding for the first time. Eggs from 201 experienced breeders had a mean period of 65.6 days (63–72); 55 eggs from inexperienced birds averaged 63.8 days (55–66).

In 1964–1965, we compared the length of the incubation periods in two other ways, disregarding temporarily the experience of the female (Figure 4): 1. All 117 eggs, laid before 1 December and presumably by experienced females (H. I. Fisher, 1969), were incubated an average of 65.4 days (61–70); 59 eggs, laid after 2 December by young females (?), averaged 64.7 days (55–69). 2. The first 50 eggs laid in the colony were incubated an average of 65.4 days; the last 50, only 64.3 days. These data indicate that eggs from inexperienced females hatch more quickly though the difference is relatively small.

During our study the Laysan Albatrosses incubated eggs from 20 November to 18 February. Ninety-seven per cent of the breeding birds began incubation before 7 December and 65 per cent by 2 December (H. I. Fisher, 1969). Only an occasional bird still incubated a fertile egg after 10 February.

The Light-mantled Sooty Albatross (*Phoebetria palpebrata*) requires 63 to 67 days (Sorenson, 1950b); the Galapagos Albatross (*Diomedea irrorata*), from 65 to 70 days (Murphy, 1936:573); the Black-footed Albatross (*D. nigripes*), 65 and a fraction days (Sheehan, 1952; Rice and Kenyon, 1962b); the Black-browed Albatross (*D. melanophris*), 71 days (Richdale, 1952); the Wandering Albatross (*D. exulans*), 78 days (75 to 82) in 163 nests (Tickell, 1968); and the Royal Albatross (*D. epomophora*), the longest of all, 79 days (77 to 81) in 35 nests (Richdale, 1952; Sorenson, 1950a).

Length of the Individual Incubation Spans

In the Laysan Albatross, both members of the pair share the incubation in fairly regular attentive periods, or spans, a span being one continuous setting by either sex. According to Hadden (1941:32): "They change off on the egg about every 18 days." Sheehan (Richdale, 1952:36, 51) reported that the female incubated the egg for 5.3 days immediately after laying it and that there were from three to six different spans during the incubation period. Rice and Kenyon (1962b:543–545) believed that the pair divided a total of seven spans and that the female's first span averaged 2.5 days.

Our data on the length of the incubation spans, shown in Table 1, include only those spans terminated by the return of the mate. The greatest number of spans in any one pair was seven, and the occurrences of Spans 6 and 7 were so few that we may say the cycle usually consists of five. Ninety-five per cent of the successfully incubated eggs hatched before Span 6 — 75 per cent hatched in Span 5; 20 per cent in Span 4. Rice and Kenyon (*op. cit.*) indicated that 82 per cent hatched before Span 6 — 57 per cent in Span 5; 23 per cent in Span 4.

The averages in Table 1 confirm, in general, the averages given by Rice and Kenyon (1962b:543, Table 8). But span lengths distant from the average unduly influence the average, and the smaller the average, the greater the bias. For example, in Table 1 some females in their first span (Span 1) sat on the egg for 32 days — 16 times the average. And one male in his first span,

TABLE 2

Relationship between Time of Hatching and Exchange at the Nest in 100 Pairs of Experienced Laysan Albatrosses*

Hatching	*Exchange to:* *Male*	*Female*
—4 days	5	3
—3	5	6
—2	2	3
—1	9	11
0 hatching	7	10
+1 day	8	5
+2	5	7
+3	4	1
+4	2	4
	—	—
Total	47	50

*No exchange occurred during this time in three pairs.

Span 2, incubated for 58 days — more than twice the average. Consequently, the median and mode in Table 1 more closely portray the true biological situation.

The modal time for Span 1 in all females is less than 24 hours; 40 per cent leave before 24 hours; from three to eight per cent leave after only 10 to 16 hours. Another 29 per cent stay less than 48 hours. Looking at it another way, four of five females (80 per cent) in their first span leave in less than 48 hours; most leave in less than 24 hours.

There is a distinct difference between experienced and inexperienced pairs in the length of Span 1. In Table 1, lines 2 and 3, experienced pairs (with eggs before 7 December) showed spans approximately half as long as those of pairs laying after 6 December.

Following Spans 2 and 3, the longest, the spans decrease in length, becoming quite short just before hatching (see Table 2). Ninety-seven per cent of the experienced pairs exchange duties within ±4 days of hatching; two-thirds exchange within ±2 days; one-half within ± one day. Either or both members of the pair may be at the nest when the chick emerges.

The averages for all birds show that the total incubation time for the male is 36±1 days and for the female, 29±1 days. The male maintains the greater role, even when the early spans are very long; the birds adjust the lengths of later spans (Table 3). In Pair 3, for example, the female's first span was five days longer than average; her mate then stayed nine or 10 extra days in his

TABLE 3

Examples of Compensating Variations in Lengths of Incubation Spans by Pairs of Laysan Albatrosses

Pair number	*Sex on duty*							*Total incubating time, days*	
	F	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*
1	2	37	24	3	—	—	—	40	36
2	1	10	18	20	11	2	—	32	30
3	6	33	21	1	—	—	—	34	27
4	1	4	10	14	16	10	2	28	29
5	3	6	17	32	4	—	—	38	24
6	8	27	26	1	2	—	—	28	36

first stint, Span 2; she stayed an extra day or so in her second span, Span 3. His last period, Span 4, was very short, but his total time on the egg was longer than the female's. Pair 6 was similar. In Pair 5, the male left 17 days early in his first span and made up for it by staying 18 extra days in his second.

The Hatching Period

In 1962–1963, 1964–1965, and 1968–1969, the first eggs hatched between 23 and 25 January. Hatching continued until 14 February in 1963, 19 February in 1965, and 15 February in 1969. Chandler S. Robbins (pers. commun.) reported that one egg hatched 20 February 1963 on Sand Island.

In the main period, 28 January through 5 February, 92 per cent of the chicks emerge. In 1962–1963, 41 per cent of the eggs hatched before 1 February; in 1964–1965, 48 per cent; in 1968–1969, 46 per cent. Rice and Kenyon (1962b:547) indicated two peaks of hatching for the Laysans — the major peak on 1 February and a lesser peak on 6 February. We find two peaks in our data but in modified form.

The curve representing egg dates skews to the left and only hints at two peaks. Since 27 November is the median date for egg-laying by old experienced females and 3–4 December is the median date for inexperienced females (H. I. Fisher, 1969), any eggs laid about 27 November would hatch about 1 February, with the peak from 28 January to 5 February (Figure 5). Although the higher rate of nest loss in young females greatly reduces the second peak, 7 to 18 February, the hatching of eggs from aged females with new mates augments the total for 9 February (H. I. Fisher, 1969).

An egg may be pipped six days before hatching (Figure 6); most are pipped from two to four days as Rice and Kenyon (1962b) noted. The sex of the attendant parent does not affect the length of the pipping period — mean days for 64 males, 2.8; for 54 females, 2.9; for 29 pairs, 3.5. Dixon (1933), Jameson (1961), Richdale (1952), Sorenson (1950a, b), and Tickell (1968) gave comparable periods for pipping in other species of albatrosses.

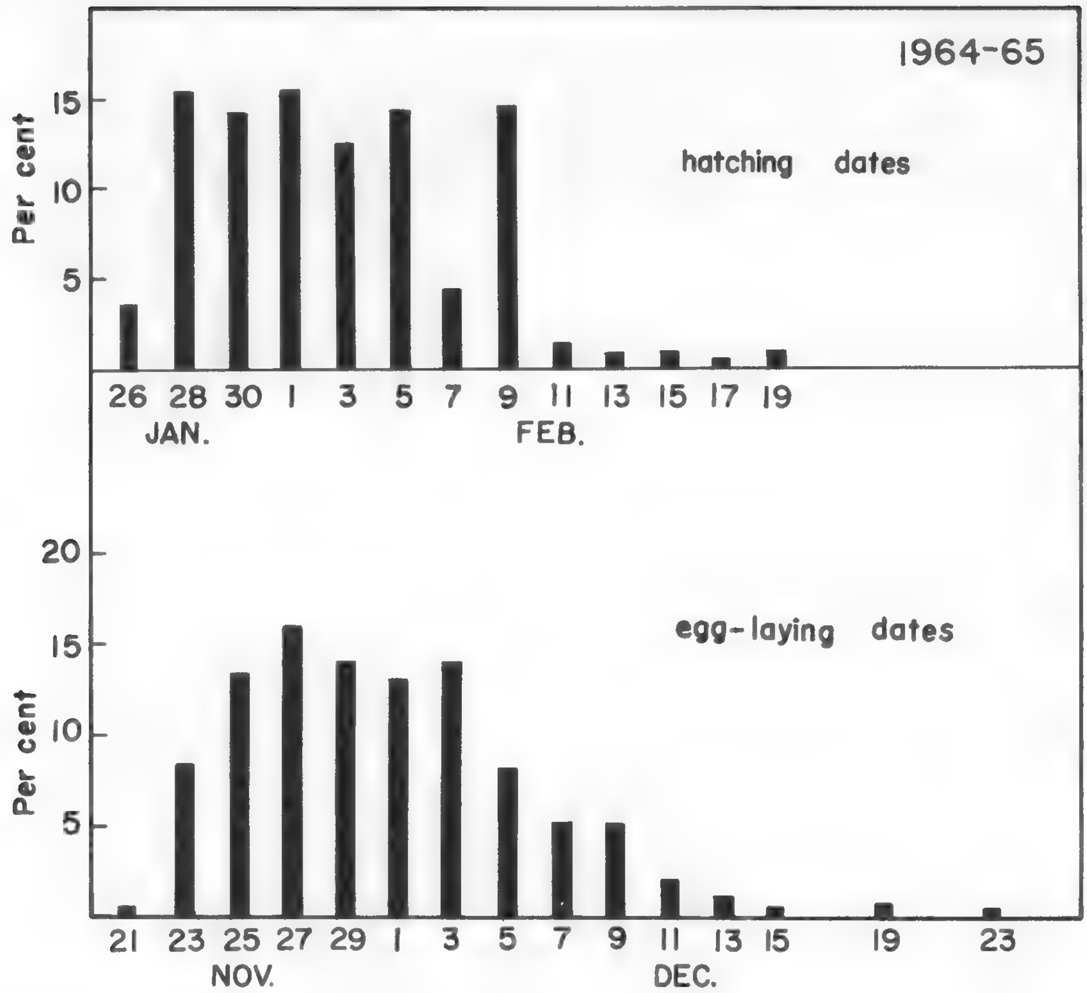


Figure 5. Comparison of the periods of egg-laying and hatching in the Laysan Albatross during the 1964-1965 breeding season.

In the Laysan Albatross we have no evidence that the adults aid hatching in any way. And we find no correlation between the emergence of the chick and the time of day. According to Richdale (1952) the chicks of the Royal Albatross hatch only in daylight.

The parents never remove the eggshells; they just trample them into the nest. Some fragments, kicked out by the scratching chick or snagged on the adults' bills or claws, appear on the outer slopes of the nest rim.

Hatching Success

The hatching success normally approximates 70 per cent (Table 4). We shall discuss later the 1964–1965 season when the success was only 56 per cent.

TABLE 4

Hatching Success of Laysan Albatross Eggs

	1962–1963	*1963–1964*	*1964–1965*	*1966–1967*	*1968–1969*
Number of eggs	626	708	350	628	475
Per cent hatched	71	73	56	61	70

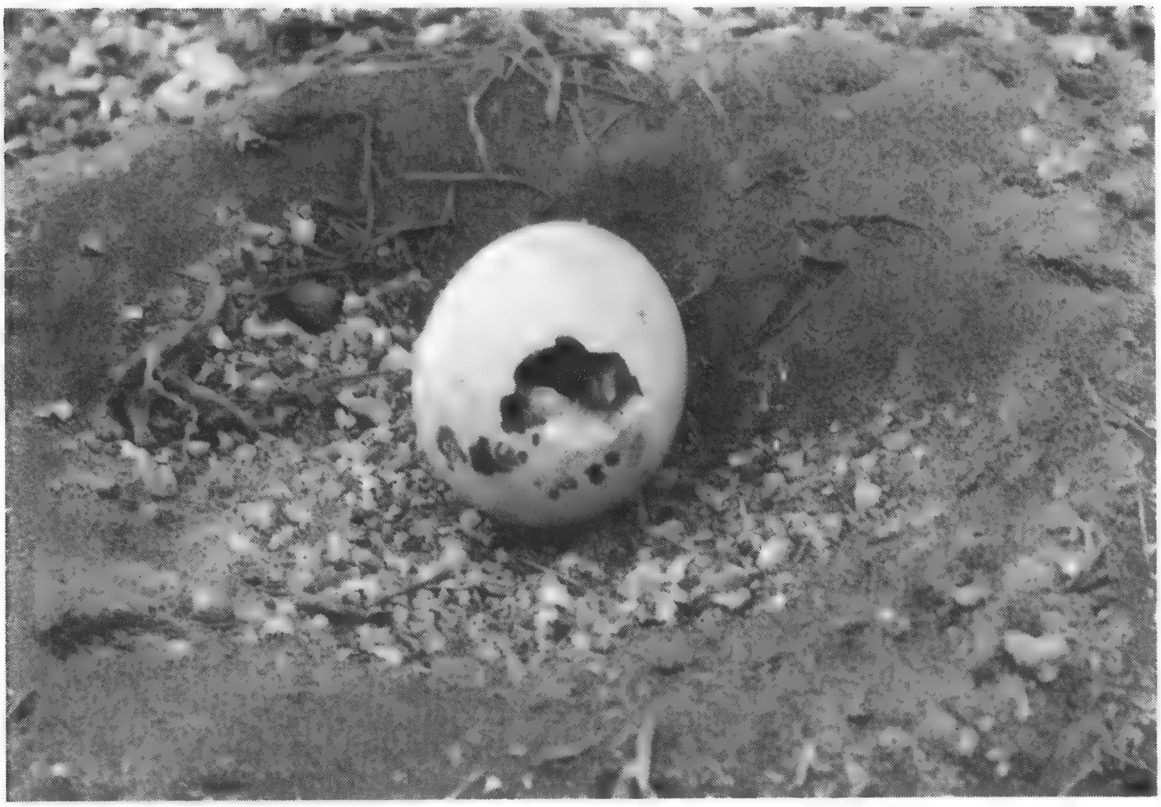


Figure 6. The chick makes a large pip in the egg and may remain in the egg for as long as six more days.

The experience of the female is often a major factor in determining the success of the nest. Table 5 shows significant differences between experienced and inexperienced females in 1962–1963 and 1964–1965.

The date of laying also seems to be a factor. More of the eggs laid the first 10 days of the egg-laying period hatch than of those laid in the last 10 days (Table 6). Some of this difference in hatching success is related to the experience of the female, as just indicated, but even in young females, 54 per cent of the eggs laid early hatch, while only 44 per cent of those laid later hatch successfully.

Experienced females laying early in the season hatch an average of 66 to 82 per cent of their eggs; inexperienced females, an average just above 50 per cent. Less than a third of all nests started the last week of the season are successful.

Examples from two years indicate the causes of this decrease in nest success as the season progresses. In 1962–1963, only nine (35 per cent) of the last 26 eggs laid after 11 December hatched. In the 17 nests that failed: the birds abandoned 10 eggs; three eggs disappeared; the birds broke two eggs; and the pairs in the remaining two adjacent nests temporarily interchanged partners and then deserted. In 1964–1965, only three (25 per cent) of 12 eggs laid after 11 December hatched. Three eggs disappeared; the birds deserted three and broke two; one was infertile.

Loss of Nests and Eggs

Many factors, each difficult to assess, affect the success of albatross nests on Midway.

The weather and number of desertions by incubating birds influence the amount of predation on eggs by house rats (*Rattus norvegicus*). The rats take mostly abandoned eggs and chicks, but do not discriminate between those

TABLE 5

Effect of Experience of Female Laysan Albatross on Hatching Success

Season	*Experienced*		*Inexperienced*	
	Number of eggs	*Per cent hatched*	*Number of eggs*	*Per cent hatched*
1962–1963	182	77	69	51
1964–1965	132	68	72	46
1968–1969	220	69	71	66

truly abandoned and those only temporarily abandoned. As we shall discuss later, eggs temporarily abandoned for as long as five days may hatch. The eating of eggs by rats, either predation or scavenging, is one factor, though slight, that lowers the population. The effect of rats on the chicks is probably negligible; chicks, so weakened that they become victims of rats, are most often those abandoned by parents and doomed anyway.

We observed Golden Plovers (*Pluvialis dominica*) eating the contents of albatross eggs. Rats or the feet of incubating albatrosses must have cracked open the eggs first because no plover could crack the thick shell.

Another minor factor in egg loss, perhaps ±1 per cent, comes from the egg rolling out of the nest. This happens when the exchange ceremonies are too vigorous, when the bird retains the egg in the pouch as it stands up or moves about, when the nest rim is so worn down that strong winds blow directly on the egg, or occasionally, when an errant wind current drops an arriving bird on top of an incubating bird. The landing bird may hit with enough momentum to push the nesting bird and egg several feet. The adults never attempt to move a displaced egg back into the nest; infrequently, if it is only a foot or so out of place they reclaim the egg by building a new shallow nest around it.

On 1 December 1966, in a restricted area on the Navy fuel farm on Sand Island, 35 Laysan and Black-footed Albatrosses died on their nests. There

TABLE 6

Relative Success in Hatching of Laysan Albatross Eggs Laid Early and Late in the Season

Season	*Laid before 28 November*		*Laid after 5 December*	
	Number of eggs	*Per cent hatched*	*Number of eggs*	*Per cent hatched*
1962–1963	—	—	26	35
1964–1965	153	82	44	40
1968–1969	235	66	47	62

were no marks on their bodies; all were in normal incubating posture except that their necks and heads drooped down the side of the nest. Clearly, nothing had molested or frightened them. The only explanation for this "kill" was that, during the windless night, poisonous fumes from the fuel had blanketed them temporarily. Similarly, in 1967, when a jet fuel line broke, "more than 75 birds died."

The direct effects of man on nests and eggs are more than occasional and include intentional slaughters of as many as 200 incubating birds in one night, the breaking of eggs by children, and the killing of birds by trucks on roads and runways and by collisions with flying planes and antennas. The death of either parent not only means that the egg is lost, but also that the survivor will not breed the following season.

Man's major roles in the destruction of nests and eggs have been the taking over of the albatross breeding grounds for his own activities and structures (Figure 7) and the elimination, during his construction work, of their nests and eggs over wide areas (H. I. Fisher, 1966).

The incubating bird itself is also a menace to its egg. With its large webbed feet and sharp claws, it crushes or punctures from one to three per cent of the eggs. At first we suspected that our activities might cause the birds to move about and break even more eggs, but a spot check outside the study area showed a similar percentage of losses from crushing and puncturing.

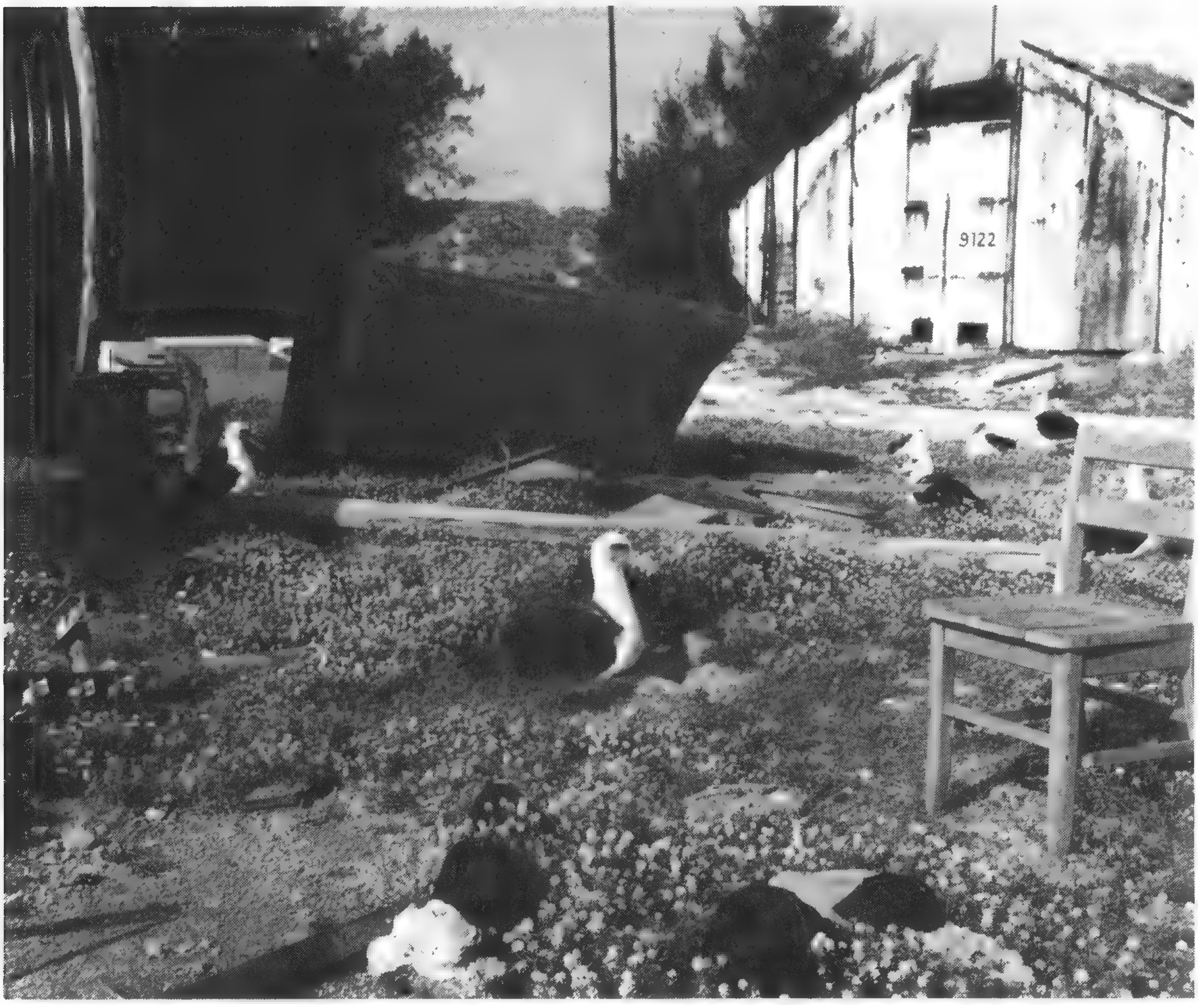


Figure 7. The debris of military activity usurped parts of the colony on Midway Atoll, but much is being cleaned up while the Laysans nest among the remaining items.

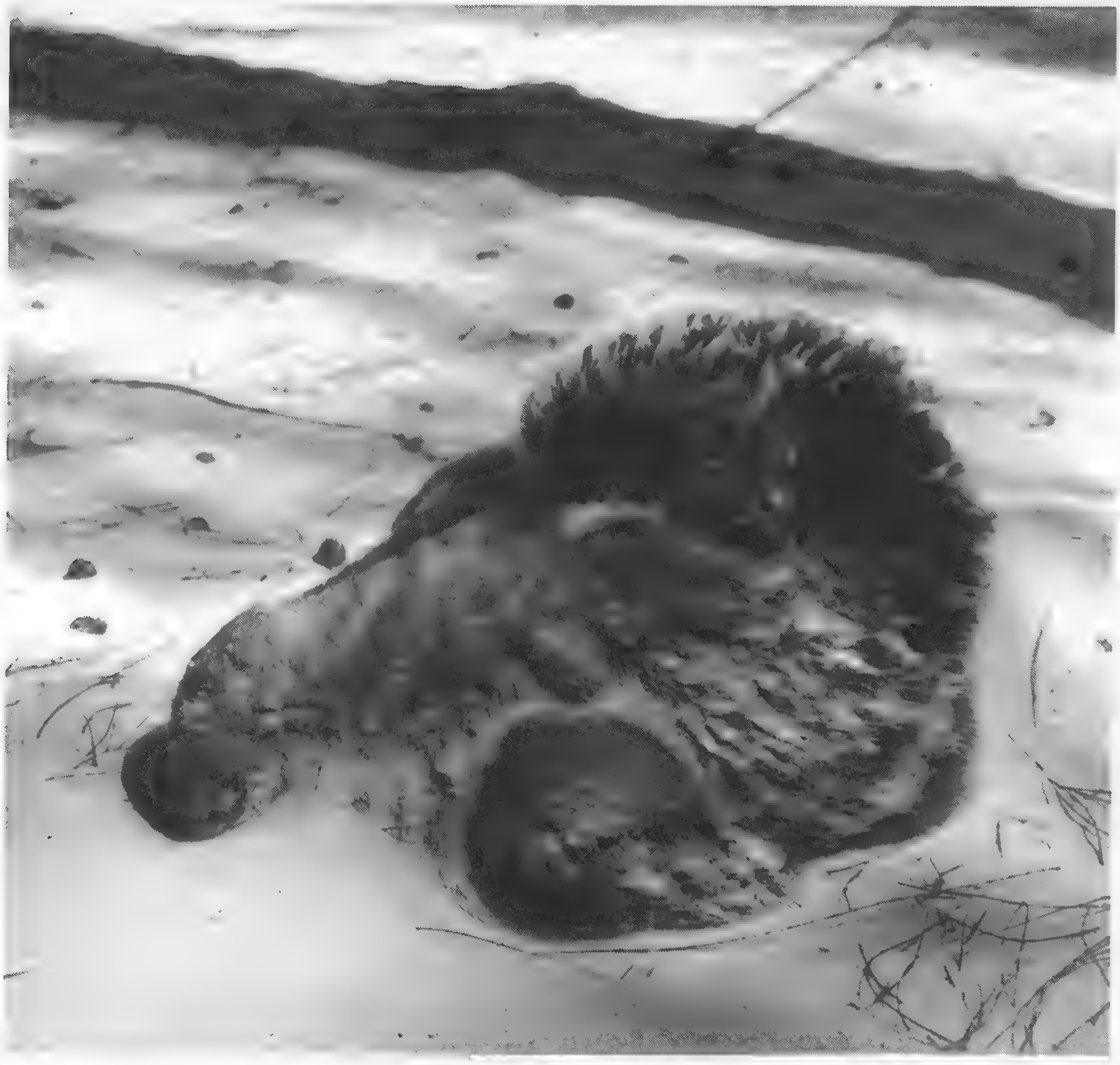


Figure 8. The wind of a storm blows fine sand into the loose down of a chick and threatens to bury it. Storms are often a major cause of mortality among young Laysans.

The breakage increases as incubation progresses and the egg shells become more fragile. Even undisturbed parents are sometimes guilty. More guilty though, as far as temporarily abandoned eggs are concerned, are the nonbreeding birds — the former breeders and the nearly mature juveniles that try to "take over" exposed eggs. Their urge to incubate is transitory. Even if they do not break the eggs, they soon desert them.

If one of the owners returns to a temporarily abandoned egg while a strange bird is on the nest, the owner soon leaves because it will seldom exchange places with a stranger and it sees no egg in the right place. Sometimes the intruder is a young female that lays a second egg. This, too, is disastrous because a Laysan Albatross cannot incubate two eggs (H. I. Fisher, 1968). Even if one egg is rolled out, as frequently happens, the temporary use of one nest by two pairs disturbs the normal sequence of nest-reliefs and eventually leads to desertion.

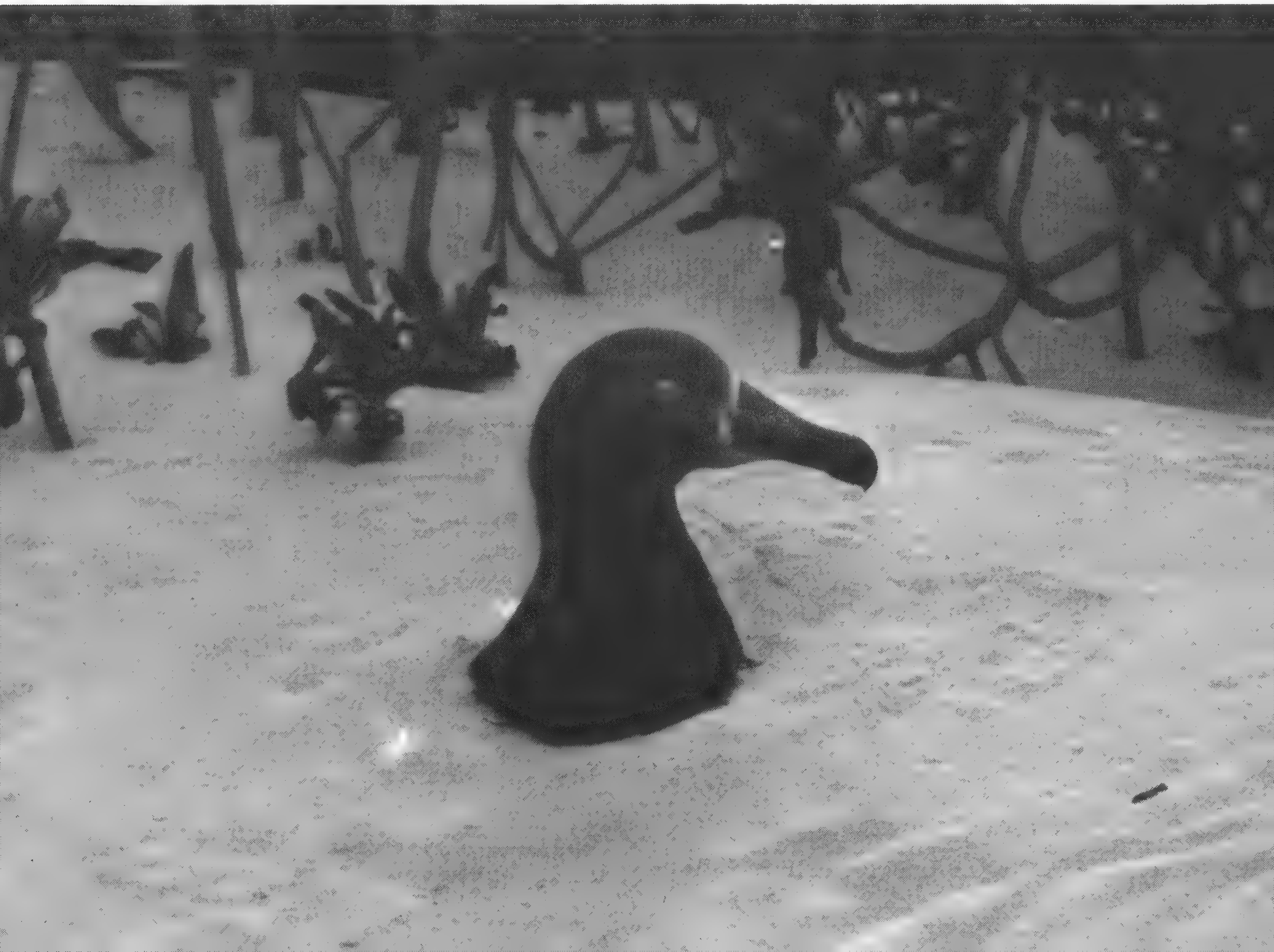
Infertility is also a factor, but we have no idea how important it is. In 1961–1962, the observed infertility was 4.0 per cent; in 1962–1963, 16 per cent in 50 eggs; in 1964–1965, 4.5 per cent in 72 eggs of young birds, and 9.8 per cent in 132 eggs of experienced females; and in 1968–1969, 3.4 per cent of 475 eggs in the colony. We regard these percentages as minimal. Undoubtedly, some of the eggs lost by other means were infertile. An infertile egg apparently breaks more easily than a fertile one. In one season, 11 per cent of 64 eggs broken by birds were infertile. This same masking also affected the data on embryos that died in the egg before hatching. However, we believe that less than one per cent of the incubated eggs contained dead embryos.

Storms with winds bearing water and sand are responsible for major losses during incubation and the early guard phase — when the young are small (Figure 8). Accompanying changes in the ambient temperature from just above 50° F to 75° F during the incubation period of the Laysan Albatross are not important. The Black-footed Albatrosses that nest on the open beaches bear more of the detrimental effects of the wind, sand, and water than the Laysans nesting in the more sheltered interior of the atolls.

However, wind velocities from 40 to 70 knots are not infrequent at this season and may blow eggs out of shallow nests or, if the sandy nest is dry, may blow the nest out from under the incubating bird. A bird rising on its nest may be pushed off backward and kept from regaining the brooding position; the egg may be dropped outside the nest. If the bird manages to get back, the wind may tip it backward again each time it rises and thrusts the belly forward to open the pouch for the egg. After three or four hours in such strong winds some birds desert. Others simply rest on top of the egg; if the storm is long, this may delay incubation.

The wind may move the sand up and around an incubating bird and imprison it so firmly that, occasionally, only its head and neck show (Figure 9). Sometimes so much sand filters into the down of a chick that it can no longer rise to beg for food.

Figure 9. Black-footed Albatrosses, incubating in the loose sand near the beaches, may be firmly imprisoned by blown sand which also invades the growths of *Scaevola* where Laysan Albatrosses nest. Photographer unknown.



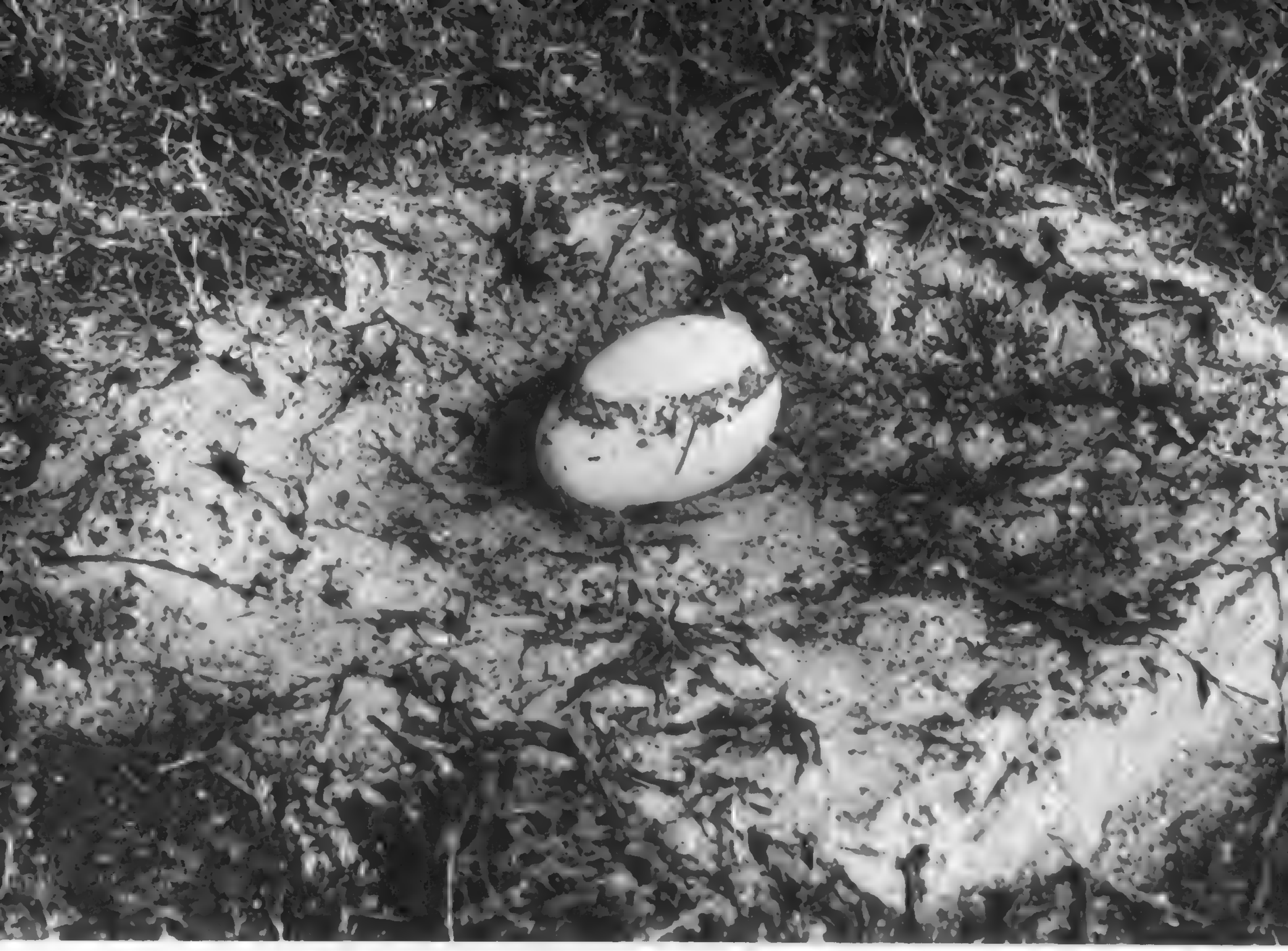
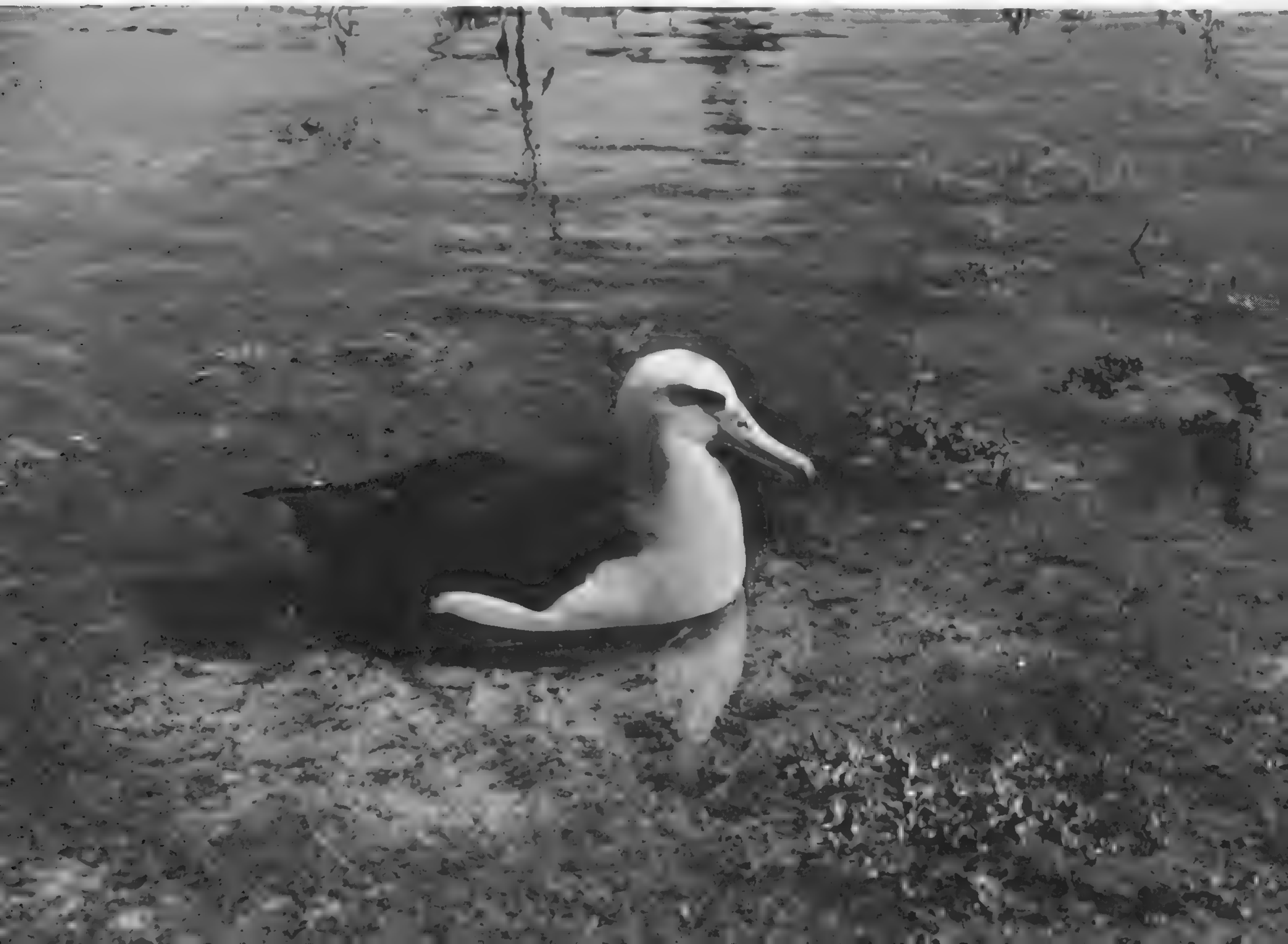


Figure 10 (*above*). Egg of a Laysan Albatross, deserted and showing the debris-marked water level of a recent flood.

Figure 11 (*below*). When nests are flooded by heavy rainfalls, some Laysans attempt to continue incubating by floating over the egg.



Seismic tidal waves or wind-generated waves that carry water inland over low-lying colonies wash eggs and young out to sea or deposit them in windrows at the high-water mark. Since the parents do not recognize their displaced egg or chick or adopt another, all are lost.

In December 1962, waves ruined 468 nests in one area of Eastern Island and 211 on Sand Island. In December 1964, a six-day storm with wind speeds of 70 knots destroyed hundreds of albatross eggs along the shores and as far as 150 yards inland on both islands.

In the low interior of Sand Island, where there is some soil with heavy grassy growth, the rain water that can neither drain downward nor move off horizontally covers the eggs and chicks. Though the egg may stay in the nest (Figure 10), the adult, if it does not desert, is helpless to do anything but float above the egg (Figure 11). On 8 December 1969, 50 of more than 200 flooded nests were marked by stakes; on 9 December, they were flooded again, making a total immersion time of 24 to 48 hours. On 15 February, we found 30 of the 50 nests deserted, nine obliterated, three with rotten eggs, and eight with healthy chicks. Thus, the greatest loss of submerged nests, 60 to 80 percent, was due to desertion; less than 20 per cent produced a chick.

Because the most important factor in egg loss is desertion, we studied it in detail from 1961 to 1966. In those seven years we identified some 2,532 birds—1,174 males and 1,358 females — incubating on 3,681 nests. Twenty-one per cent — 260 males and 272 females — deserted; 17.9 per cent deserted once; 3.1 per cent, more than once. There was no significant sexual variation in the frequency of desertion.

An analysis of the data on repeated desertion by 78 birds revealed that one-third of these albatrosses completed incubation only half the time, and 60 per cent completed incubation roughly two-thirds of the time. Of these 78 birds, 72 abandoned their eggs during two breeding seasons, five in three years, and one in four years. Eight birds — five males and three females — deserted all the eggs that they or their mates were responsible for laying; all eight were birds that started breeding during the seven-year observation period.

In 1962–1963, with 615 nests in the study plot, some 197 birds — 98 males and 99 females — abandoned their nests and eggs during incubation. Table 7 shows the chronology of desertion according to the span of incubation by each sex. It reveals that two-thirds of the desertions took place during the long three-week spans (Spans 2 and 3). The number of desertions during Spans 1

TABLE 7

Laysan Albatross: Time of Desertion by Span of Incubation, 1962–1963

	Span and Sex					
	1–F	*2–M*	*3–F*	*4–M*	*5–F*	*6–M*
Instances	31	66	62	31	6	2
Per cent of total	16	34	31	15	3	1

TABLE 8

Laysan Albatross: Day of Span and Percentage of Desertion in 1962–1963

	Span and Sex					
	1–F	*2–M*	*3–F*	*4–M*	*5–F*	*6–M*
Modal length of span in days	1	23	20	14	8	5
1–5	61.3	51.5	41.9	38.7	83.3	100
6–10	6.5	12.1	22.6	35.5	16.7	0
11–15	19.3	12.1	12.6	16.1	0	0
16–20	9.7	10.6	12.6	3.2	0	0
21–25	0	7.5	8.1	0	0	0
26–30	3.2	3.0	0	0	0	0
31+	0	3.0	0	0	0	0

and 4 were equal despite the fact that the average length of Span 1 was one or two days and that of Span 4 was 14 days.

According to Table 8, most desertions occur soon after the bird assumes incubation in any span, and the number of desertions decreases clinally thereafter. Desertions after the average length of the span constituted 71 per cent by the female in Span 1; 9.1 per cent by the male in Span 2; 8.1 per cent by the female in Span 3; and 9.7 per cent by the male in Span 4. Altogether, these desertions constituted only 17.8 per cent of all desertions.

TABLE 9

Laysan Albatross: Egg Loss by Date When Eggs Were Laid in 1964–1965*

	Eggs		*Per cent loss*	
	Laid	*Lost*		
November 21–23	30	6	20.0	17.1
November 24–25	46	7	15.2	
November 26–29	107	46	43.0	45.5
November 30–December 3	95	46	48.4	
December 4–7	44	16	36.4	40.3
December 8–11	23	11	47.9	
December 12–15	4	3	75.0	80.0
December 16–23	1	1	100.0	

*Infertile eggs are excluded.

I should mention here that we found only one instance of a pipped egg being deserted.

Despite the concentration of desertions in Spans 2 and 3 and in the early days of all spans, the desertions are, with some exceptions, fairly evenly distributed throughout the incubation period of the colony (Table 9).

Stormy weather causes birds to desert. In 1962–1963, 26 per cent of all desertions were associated with severe storms; two of these storms occurred during the egg-laying period and caused the high loss shown in Table 10. In 1963–1964, a season with no major storms, the desertions were evenly distributed. In 1964–1965, 38 per cent of all desertions occurred during three storms; in 1965–1966, 24 per cent took place during a single storm. From 1966 to 1969, there were no major storms during incubation and no peak periods of desertion.

TABLE 10

Extent of Egg Loss by Laysan Albatrosses during the Egg-laying Season

	All eggs in plot			*Eggs laid 7 December or later*		
Season	*Total number*	*Number lost*	*Per cent*	*Total number*	*Number lost*	*Per cent*
1961–1962	378	25	6.6	—	—	—
1962–1963	626	84	13.4	26	17	65.4
1963–1964	708	24	3.4	139	9	6.5
1964–1965	350	56	16.0	52	31	59.6
1965–1966	749	28	3.7	85	3	3.5
1966–1967	628	34	5.4	115	5	4.3
1968–1969	476	47	9.9	48	1	2.1
1969–1970	776	40	5.1	65	5	7.7

Thus far the discussion has been of the usual pattern of desertion — the incubating bird leaves, the nest is unsuccessful. However, we also found that it was not unusual for a returning bird to abandon when it does not find its mate on the nest. In 1962–1963, 33 of 195 desertions were this type; the eggs were uncovered anywhere from one to 26 days. Mates, returning to cold eggs that had been exposed from one to 26 days, incubated an average of eight days (1–31) before deserting. In this behavior there was no difference between the sexes, but most of the pairs involved consisted either of two young birds or a young and an old bird.

We saw 11 instances of still another pattern of desertion in which the incubating bird departed, stayed away from two to 18 days (average of 5), then returned and resumed incubation before its mate came back from the sea.

Of 122 pairs, of which one or both members deserted in 1962, 93 (76 per cent) had an egg the following year; 15 (12 per cent) did not nest the following year; and 14 (11 per cent) were not recaptured in the two following years. Seven of the 93 birds that began nesting the following year deserted again; four of these were in their second breeding season. We believe that 13 of the 15 that did not nest the second year lost their mates in 1962–1963 because they had new mates in 1964–1965. We know that five of the 14 not recaptured died and think that seven others also died because their mates had new mates in 1964–1965.

We may summarize the reasons for desertion as follows:

Cause	*Percentage*
Nest too close together	1–3
Eggs broken by parents	2–4
Eggs missing from the nest	5–8
Failure of living mate to return on time	10–20
Death of mate	1–3
Interference by second pair of breeders or juveniles "taking over"	1–4
Mix-up of pairs from adjacent nests	0–1
Storms	0–38
Unknow	10–30
Our handling	2–4

Although there is an overlap of the direct causes of egg loss such as rats and the indirect causes such as desertion because of our handling, we may estimate the direct effect of each factor in relation to the percentage of eggs laid. These estimates apply only to Midway for the years stated:

Cause	*Percentage*
Desertions for all reasons	20–30
Storms	0–5
Our activity	1–3
Infertility	3–16
Man's direct effect	2–5
Interference by other albatrosses	1–2
Rats	fraction
Death of embryo	fraction
Loss of mate	fraction

Figure 12 and Table 9 show the time of the impact of these factors. Evidently, after the main period of egg-laying, the rate of the losses is constant except for an increase during storms and a slight decrease during the main hatching period.

Aside from catastrophic losses, the nest failure in the Laysan Albatross averages three to six per cent during the egg-laying period (Table 10), approximately half that estimated by Rice and Kenyon (1962a:372) for the last month of the incubation period.

Copulation

We include here our observations on copulation because it is the most obvious behavior in the first two or three weeks of the incubation period, because the time between copulation and egg-laying is relatively constant and

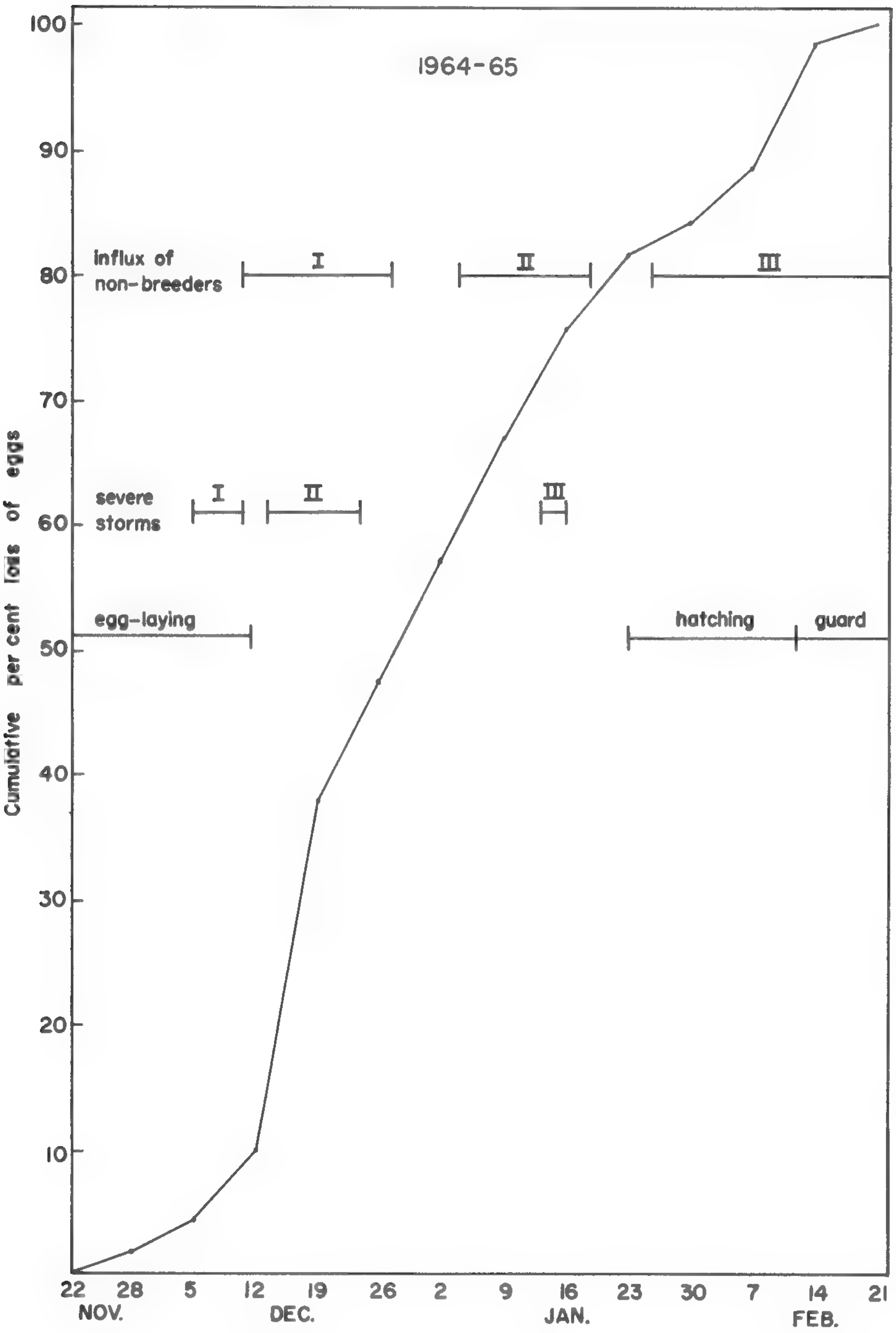


Figure 12. The cumulative impact of nest loss, in relation to weather and the biological activity of the colony as a whole.

establishes the chronology for the remainder of the reproductive period (H. I. Fisher and M. L. Fisher, 1969), and because the observations on the time, site, and age at which procellariiform birds copulate seem to be confused. Students, unaware of the exact age and breeding status of their subjects, apparently have also not distinguished between successful and unsuccessful copulations.

Our observations may clarify the information, at least for this species, because we knew the ages of many of the Laysan Albatrosses in the plot, their status — juvenile, associating, paired, breeding, formerly breeding, etc. — and their success in breeding over a nine-year period, and because we made postcopulatory examinations of many birds.

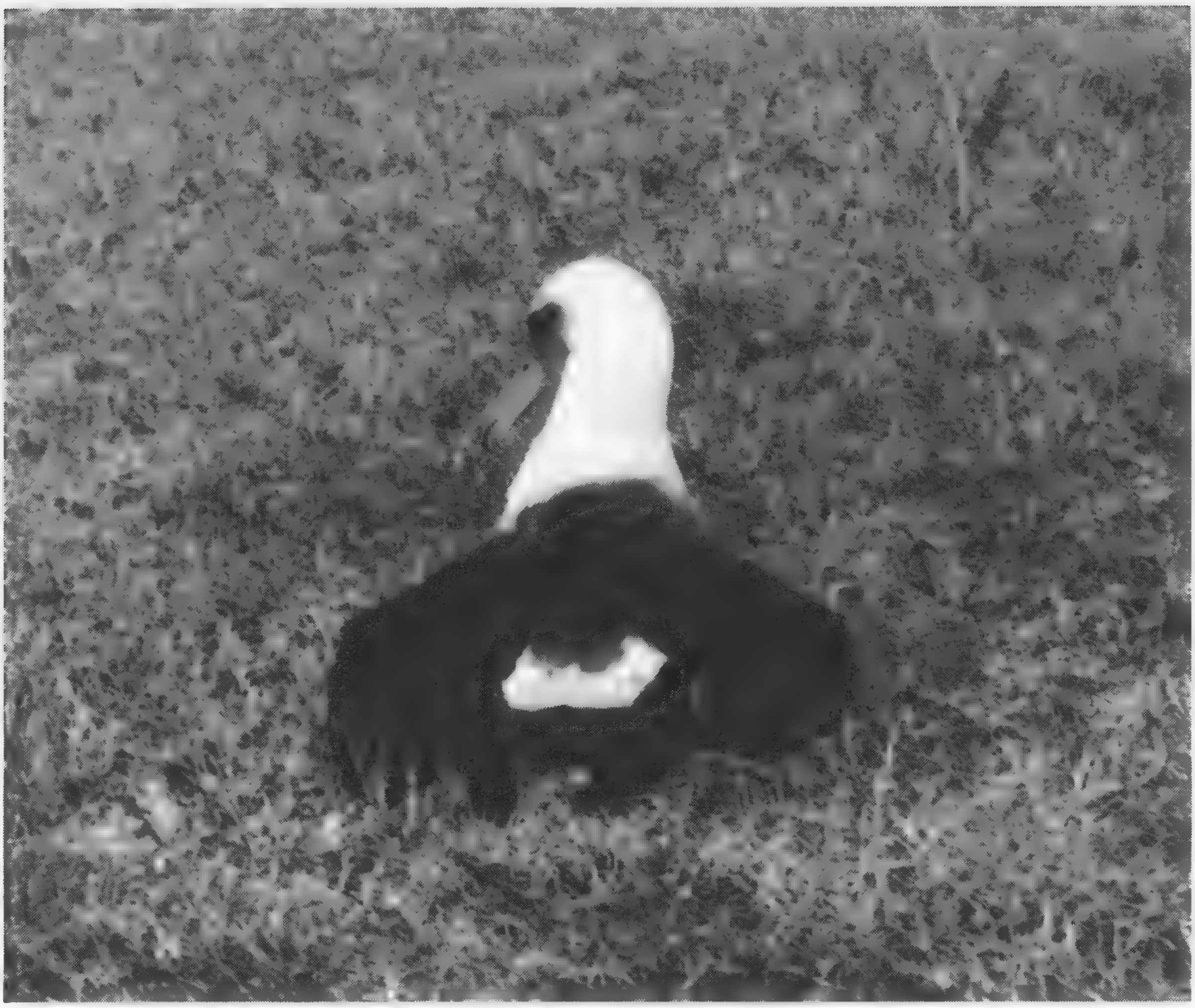


Figure 13. The female flattens her back and slightly spreads the primaries when she is ready to copulate. In this unusual instance the male has interrupted his precopulatory action to chase a nearby male, and the female is temporarily alone.

The urge to copulate is especially strong in male Laysans; even males with broken wings persist until successful with their mates. Experienced breeding males, on station and waiting for their mates of previous years and, occasionally, even males with mates beside them attempt copulation with any albatross, male or female, whose posture indicates submission. A male may run 10 or 15 yards to attempt copulation.

One must, therefore, distinguish between the true, successful copulations between mates and the unsuccessful copulations we call "rape attempts."

Precopulatory Signals and Responses

Despite the direct observation of hundreds of birds and the careful study of several slow-motion films of precopulatory behavior, we did not always see the signals that we expected. Richdale (1950), J. Fisher (1952:332), and others noted the absence of these signals in other species of Procellariiformes; some students never mentioned them.

In a pair of Laysans, the age of each bird and the length of time they have been paired are important in determining the amount of precopulatory behavior. Guhl (1961) noted that acquaintance with the mate facilitates successful breeding, at least in Domestic Fowl (*Gallus*). If such acquaintance is a factor in albatrosses, the two-year prebreeding association of members of a pair (H. I. Fisher, MS) is perhaps of major importance. Subsequent association during breeding furthers this acquaintance and lessens still more the need for precopulatory behavior. Thus, inexperienced albatrosses should show the most precopulatory behavior and the older, more experienced birds, the least or none at all. And this is true.

This acquaintance factor may operate outside the pair-bond, as, for example, between Laysans spending weeks on nests less than a yard apart, and may thus explain some of the aberrations in the fairly strict monogamous bond we associate with albatrosses.

Ornithologists, more familiar with land birds where life events pass rapidly, often assume that copulation follows courtship immediately. Courtship, as used here, refers to the complex of acts, the ceremonies and "dancing," that precede pair formation, and not to the precopulatory acts that are usually simpler and briefer. Laysan Albatrosses court and pair nearly two years before they breed, and their age and experience in breeding determine whether any part of the courtship ceremony precedes copulation.

Generally, no courting or dancing occurs immediately before copulation as Hadden (1941:30) concluded for the Laysan Albatross, Richdale (1950:40) for the Royal Albatross, and J. Fisher (1952:332) for the Fulmar (*Fulmarus glacialis*). However, pairs nesting for the first time and, more often, those that will nest the following season may dance before copulating.

In the most frequently noted "signal of intent," the male approaches a standing or resting female on tiptoe, raising his head as high as possible above hers and thrusting out his breast. To human observers, his actions indicate an attempt to dominate. He may actually push against her with his breast or try to touch her breast with his bill. Often he puts his bill over her back and shoulders just before he mounts.

From time to time both sexes utter *eh eh*, which in this context we consider a recognition of sex, mate, and non-aggression in the other bird.

The female, if she responds, may rise to full height with head up and then lower her body. She may throw bits of nest material. She then lowers her head, flexes her legs, and, with bill pointing toward the ground, flattens her back by slightly spreading the scapular and primary feathers on either side (Figure 13).

Just as the male's bill-over-neck act is his final and most potent signal, her responses of greatest willingness include non-aggression at his touch and the slight squatting posture with the primaries spread. Her squatting posture may be as much a physical as a psychological signal in that it provides a broader and more secure base for the male's large, widely separated feet.

We found experimentally that males do not attempt copulation with a female that cannot spread and droop her wings. Later, a natural event verified this. When a male, his right wing broken so that it drooped out and down slightly, made his way through the colony, the males on his right that could see the drooped wing attempted copulation with him while the males on his left ignored him. The sight of the drooping wing was apparently sufficient, by itself, to stimulate the males.

Copulation between Members of a Pair

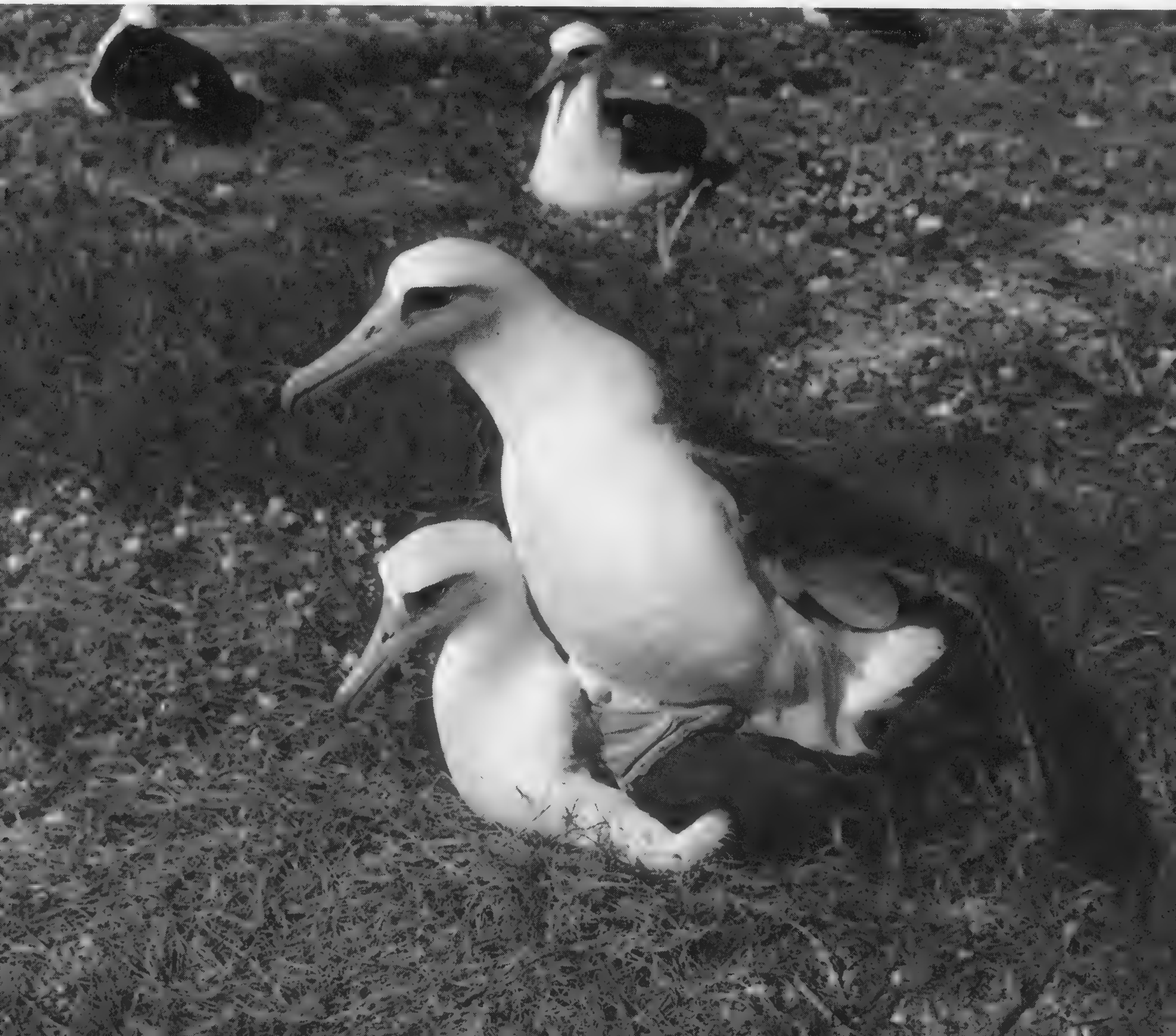
The first copulations occur within hours of the arrival of the first experienced females and reunion with their mates, usually in the second week of November, and at any time of day. We observed few copulations after 8 December. Tickell (1968:19) stated for the Wandering Albatross and H. I. Fisher and M. L. Fisher (1969) for the Laysan Albatross that copulation preceded the laying of the egg by eight to 10 days; Richdale (1950:36) indicated 10 to 29 days for the Royal Albatross and added that the female Royal returned periodically to the colony ". . . only at the dictates of an urge for coition." Kirkman (1937:197) stated that there may be a 30-day period in the Black-headed Gull (*Larus ridibundus*).

The Laysan female, if she arrives at the colony before her mate, which is unusual, may make one or two brief forays back to sea. Ordinarily, she joins her waiting mate; they copulate and return to the sea together.

In old experienced breeding birds, copulation often takes place within an hour or so of their reunion (Figure 14). Birds breeding for the first or second time, may not copulate for several hours or until the following day.

Laysans may copulate on the future nest site, the male's nest scrape, or a partly built nest, but always within his home station. Yellow-nosed Albatrosses (*D. chlororhynchus*) copulate on the nest (Rowan, 1951); Royal Albatrosses frequently copulate on the nest site, but sometimes "yards away. . . ." (Richdale, 1950:40); Light-mantled Sooty Albatrosses may copulate far from the nest (Downes *et al.*, 1959:67). The difficulty with these statements is that we do not know whether the birds were associating, newly paired, or experienced, or whether "away from the nest site" was still within the male's home station.

Figure 14. True copulation is a quiet and undisturbed act even though other males are nearby. Experienced breeders often copulate within an hour of their reunion at the beginning of a new season.



The hallmark of true copulation between paired Laysans is the subdued level of behavior and the absence of interruption by other males. A male takes no notice of true copulation only two yards away, yet he may run 10 yards for a rape attempt. The reason may be that he is aware of the copulating male's dominance on his home station and of the station boundaries. However, a male attempting rape never hesitates to cross the stations of two or three other males, probably because they, too, are away, participating in the frenzied uproar.

Actually, such large birds, living so close together, may need undisturbed copulation for successful insemination, and the absence of interference may be a behavioral adaptation to permit it.

The following description is directly from my field notes:

> Female flattens on ground with humeri separated an inch or so from her shoulders; elbows, primaries, and tail flat on the ground; male walks on from rear, up flattened tail, and onto her back, feet in middle of her back; she nibbles at sticks on ground; male crooks head and bill down toward female's head but does not touch; he treads her back a dozen times as his feet move laterally until toes flex (grip) over leading edge of upper part of wing; female's bill forward at 45-degree angle with ground, head and neck slightly extended; male extends wings partly at shoulders and elbows, 50 per cent flex at wrists; leading edge of his primaries on ground to balance and prop him as he raises front end of body; he tilts tail clockwise until its flat plane is vertical and swishes it across her tail, several times; she rotates her tail counterclockwise and cloacal contact is established as male lowers the rear of his body still further; male makes six or eight slow thrusts and rests; female terminates it by raising front of body; male is dumped off posteriorly.

Often, the female becomes the aggressor, sometimes even grasping the male's bill and yanking him off her back. In such extremes, the male, without retaliating, may give a "victory" cry, a signal of his continued dominance.

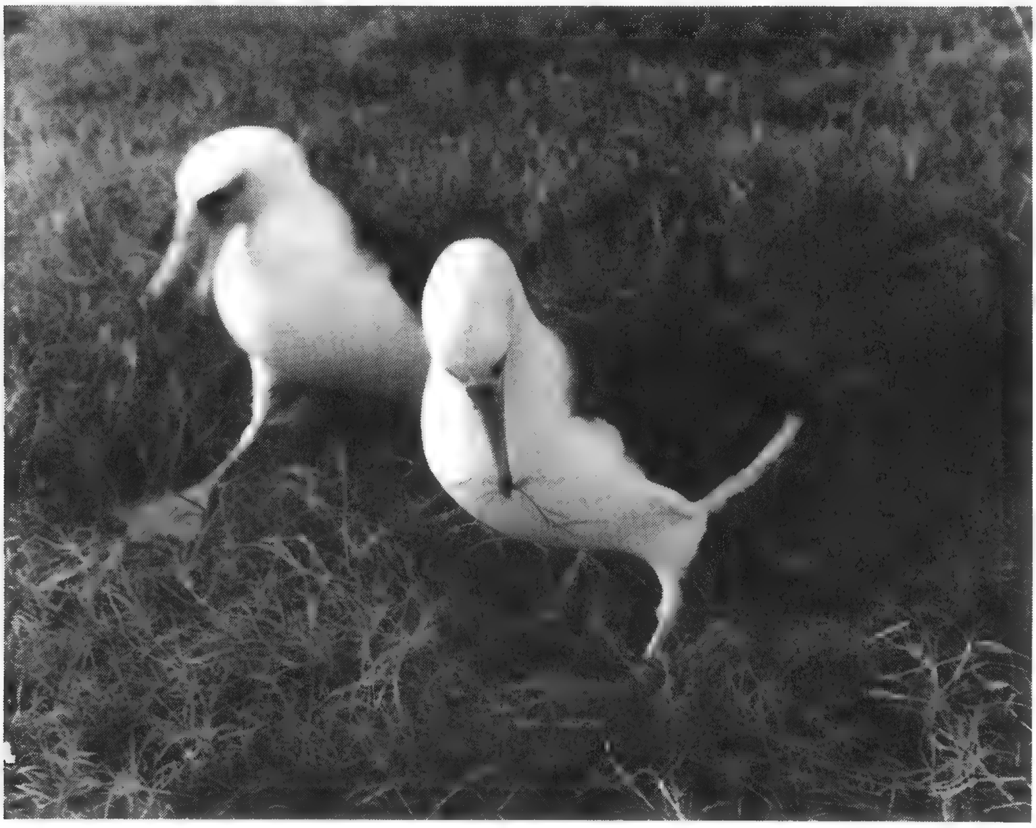


Figure 15. Postcopulatory behavior includes throwing of nest materials by the female and circling by the male.

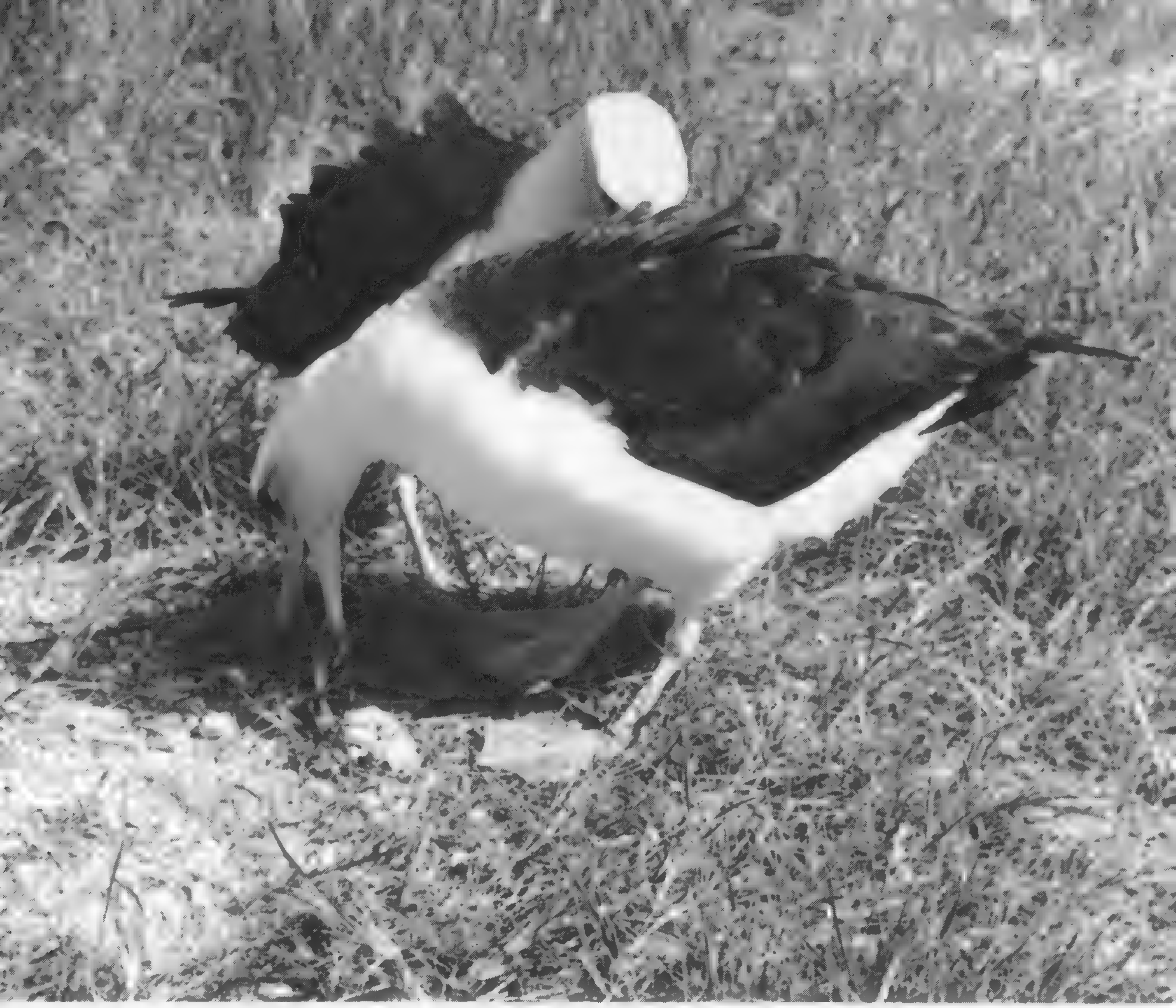


Figure 16. After copulation both members of the pair may circle and *eh eh* with bodies horizontal and bills pointed toward the ground. The male's head is usually held higher than the female's.

Most copulations last only two or three minutes. Successively completed copulations are infrequent and usually occur after an hour or so. However, if the female does not pull or slide the male off after the first cloacal contact, he may rest a moment or two, and renew his thrusts for a second contact. There are reports of Royal Albatrosses copulating several times at half-hour intervals (Sorenson, 1950a), of Light-mantled Sooty Albatrosses copulating twice in 20 minutes (Downes *et al.*, 1959:67), and of Yellow-nosed Albatrosses copulating three or four times at half-minute intervals (Rowan, 1951). I believe Rowan confused thrusts with cloacal contacts.

Postcopulatory Activities

As soon as the male dismounts, the female shakes and preens, and the male circles her, *eh ehing* (Figure 15). They bill touch. He may preen briefly or run his bill through his breast feathers in typical displacement action. Both may circle the site, pointing their bills toward the ground and *eh ehing* (Figure 16); both may throw nest material. If she resumes preening, the male may utter a soft sky *moo*. One or both may clack the bill once or twice softly.

Eventually the pair rests side by side, facing in opposite directions or towards each other with heads side by side. They touch bills and mutually preen necks, chins, and backs of heads, nibbling gently. They may continue this for an hour or so until one or both tuck the bill into the scapulars to rest, or until they leave for the sea — most often within two to five hours after copulation.

This postcopulatory period firms the pair-bond. The period of reunion, copulation, and postcopulation, along with the interval at sea, the "honeymoon," is probably the longest time that a pair of breeding albatrosses ever spends together in behavior centered on themselves. Even though they meet later in the season for nest-relief and occasionally at chick-feeding, each is then directed more toward the nest and the egg or chick than toward its mate. Of course, the concept of the importance of this time together presupposes that each searches alone for food for itself and the chick, a task that probably permits little if any "togetherness."

General Comments on Copulation

With one exception, we never saw a male Laysan Albatross copulate with an incubating female, even his mate. Murphy (1936) reported male Wandering Albatrosses copulating with females on adjacent nests in their mates' absence, and Warham (1962:147) observed copulation in the Giant Petrel (*Macronectes giganteus*) when the female was on the egg, but Richdale wrote that no such behavior occurred in the Royal Albatross (1950) or Buller's Mollymawk, *D. bulleri* (1949a, b).

Richdale observed no copulation between members of the pair in the Royal, Buller's, or "petrels" after the egg was laid, which is also true of the Laysans. Sir Hubert Wilkins (Murphy, 1936) saw "much" post-egg copulatory action in the Wandering Albatross, but the report does not indicate whether the copulating birds had eggs or were even breeding that season. One might expect the male Laysan to attempt copulation with incubating females because of their slightly drooped and spread wings. Two things may inhibit him: the female, atop her six- to 10-inch-high nest, is above him, and she usually holds her head up when he is near.

Male Laysans seldom copulate successfully with females other than their mates. Wandering Albatrosses may; Tickell (1968:20) believed that unpaired birds copulated with paired birds and that members of different pairs copulated. This may be true of Wanderers and for three years — until I distinguished between true and attempted copulations — I believed the same about the Laysans.

Experienced Laysans, not currently breeding, may copulate very occasionally and only with each other during the two-month incubation period, as do the Wanderers (Tickell, 1968:20), the Royals, and the "petrels" (Richdale, 1950).

We saw no copulation among juveniles less than six years old, paired or unpaired, but a few five- and six-year-old birds do breed. Juveniles, more than six years old, seldom copulate until the year before they nest and then only rarely and only with the mate. Wilkin's observation of post-egg copulation in the Wandering Albatross may well refer to juveniles. Once we saw a juvenile try to copulate with a three-month-old chick.

Rape Attempts

When a number of males, mated or unmated, rush at and attempt to copulate with a bird of either sex, we call it a "rape attempt." The difference between true copulation and a rape attempt is the number of birds taking part, the noise, and the fighting. True copulation is quiet and subdued. Male Laysans do not run to copulate with their mates, and observations of such activity in the Wandering Albatross (Tickell, 1968:9) and Buller's Mollymawk and the Royal Albatross (Richdale, 1949a, b; 1950) very likely relate to rape attempts.

A male or female, which, because of accident or incidental events, simulates one or more of the female precopulatory signals, may evoke rape. A broken leg that causes the body to droop between steps, a broken wing that depresses the primaries, or even a momentary stumble over a stone that throws the bird into a copulatory position may start the attempt. Males run from their stations to mount the bird, which may already be out of copulatory position and fleeing. The closest males often try to throw a running bird off balance by hooking the bill across the back of its neck. When one male mounts it, another pushes him aside and mounts. In the frenzy, there is no sex recognition; the precopulatory signals, whatever they are, override it. Males mount males, sometimes piling four deep until the stack falls over; other males rush in to mount any untangling males that have slipped into submissive positions. By this time, usually, the original victim, if a female, has scurried away ruffled and exhausted but "virgin." If she is very mussed or limps a bit, a new group may try to mount her.

One female, attacked four times in 10 minutes by four different groups of males, finally escaped and, after resting for about 15 minutes, started for her mate, nearly 80 feet away. With her left eye gone and her left wing drooping she managed to run from a fifth group of males, only to be almost smothered by a group of six more, only 20 feet from her mate.

I never determined whether males unknowingly participated in such attacks on their own mates. I see nothing to prevent this if the attack is within 25 feet of his station and begins before he recognizes her. Nor have I observed a male attempting to defend his besieged female.

Most rape attempts occur in the pre-egg stage, between 10 and 25 November when 95 per cent of the birds in the colony are experienced breeders (H. I. Fisher and M. L. Fisher, 1969). With few exceptions the birds involved are experienced breeders; the exceptions are often the victims.

We inspected hundreds of males and females after these attacks, using cloacal smear and gross examination, and found no evidence of cloacal contact, no mucous exudate or sperm that indicated successful copulation or even ejaculation.

I cannot even speculate as to the reason for the persistence of this behavior, in which I see no advantages and some disadvantages. The absence of insemination removes the possibility that rape attempts increase the number of fertile eggs through insemination by several males. Yet the advantages, whatever they are, must be stronger than the disadvantages or the rape attempts would have vanished.

Monogamy in the Laysan Albatross, perhaps like that in the Black-browed Albatross and the Gray-headed Albatross (*D. chrysostoma*), has a "degree of promiscuity" (Tickell and Pinder, 1966:128). Monogamy, strict in the female, is physical not psychological in the male. The female preserves the monogamous bond by her lack of cooperation with any male other than her mate.

Stages in the Cycle of the Colony

The colony as a whole shows several "stages" of behavior during the incubation period:

The pre-egg stage, 1–20 November: The number of experienced birds increases (H. I. Fisher and M. L. Fisher, 1969). The lone males are noisy and prone to attempt copulation with any passing male or female. The reunited pairs, though relatively quiet, add to the background sounds and action.

Mid-November through the first week of December: The breeding pairs depart for the interval at sea and return silently. Each female lays an egg, incubates for a short span, and leaves. Many males assume incubation duties, Span 2. All the birds to breed that season have arrived; 97 per cent of the eggs are laid (H. I. Fisher, 1969). Males outnumber females 15 to one. With few of the younger birds yet present, the colony is quieter.

The first two weeks of December: A few females return for their second span, Span 3. Males outnumber females two to one. With territorial and nest-spacing disputes resolved for the season, the incubating birds are even quieter. Longer incubation spans reduce the traffic of exchanging birds.

Late December: With the first influx of young birds that will breed the following year, noise increases.

Early January: The noise, traffic, and general activity increase with the first arrivals of birds that will still not breed for two more years (H. I. Fisher and M. L. Fisher, 1969).

Mid-January: The breeding birds again contribute to the increased activity. As the incubation spans shorten just before hatching, the traffic increases; more pairs are together at the nest and they are more vocal.

General Behavior in the Colony

The individual bird returns for each span of incubation alert and vigorous. It works on the nest and reacts swiftly to other albatrosses, dogs, and people. As time passes, the bird, becoming less sensitive and responsive to its surroundings, either sleeps with bill tucked into the shoulder feathers or sits staring straight ahead with the nictitating membrane pulled over closed or partly closed eyes (Figure 17).

Frequently, people can fondle such a bird. It ignores passing albatrosses which do not pause to disturb it. Whether this lassitude is an adaptation to conserve energy in the long incubation spans is a moot point. There is no doubt that during this time the bird uses less energy in activity and dissipates less as heat on convection currents set up by movements.

Only a few things fully alert the bird — a sudden sharp contact with a human being or a blow from a landing albatross; a prolonged disturbance by a neighboring bird, which it threatens by clacking its bill; or the return of its mate. Most birds turn to face strong winds or driving rain, perhaps because the normal sleeping position — head turned back with bill under scapulars— permits the wind to ruffle the feathers of the head, neck, and body, and the rain to soak the feathers. Still, some birds remain broadside to all but the very worst storms.

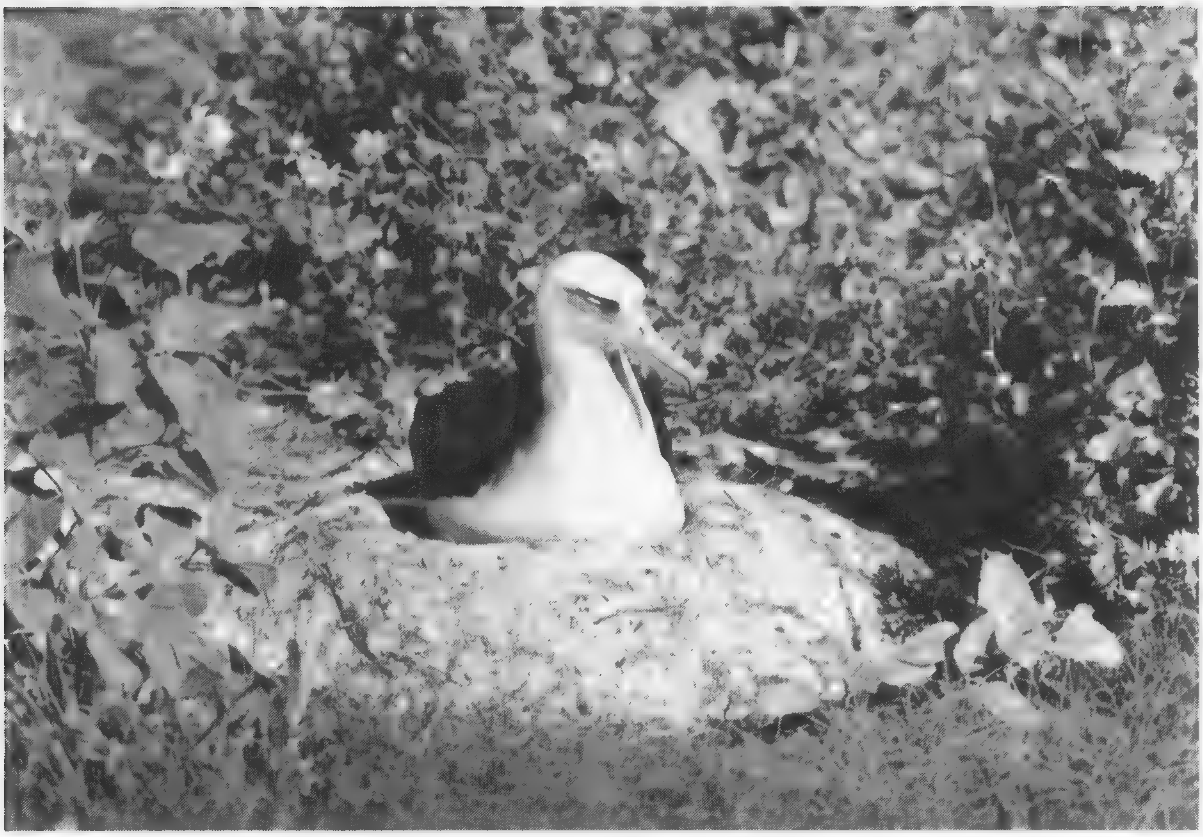


Figure 17. Incubating Laysans may pass into an "incubating trance," eyes closed.

Nest-building

Most of the construction occurs during incubation. Excluded here are the nests without eggs — the scrapes of juveniles and nests of old males waiting for their mates.

In the hours immediately before laying the egg, the female lies on the sand or dirt substrate, first on one side and then the other and, scratching with one foot, rotates constantly to produce a flat, saucer-like depression (Figure 18). When she lies on fluffy grass, the scrape may be only a hollow formed by the weight of her body. In either situation she does relatively little, if any, work with her bill.

The male builds the nest to its final dimensions during his first span on the egg, and all with his bill and the shifting of his body (Figure 19). In a sitting position, he stretches his neck out from the nest, fills the tip of his bill with material — sand, dirt, leaves, small sticks, or weed stems — and either tosses or lays it carefully along his flanks. Sometimes he hooks sand and dirt with his bill and slowly pulls it toward him. After a few minutes in one position, a rotation of a few degrees provides new material and space for it on the rim and helps shape the inside of the bowl.

As he scrapes and throws material alongside his body, some dirt and sand falls inside the nest bowl; the egg, instead of being covered, rises with the buildup. The bird's feet, with the webs between toes two and three of one foot overlapping the same webs of the other foot, support the egg. As the bird rotates, it slides its feet onto the new material, and the egg simply rolls up and onto the higher surface.

When the nest is several inches high and the materials are damp as from a rain, the bird tamps them firmly and trowels the outer surface with the flat side of the bill. The troweling produces a smooth, slick surface resistant to erosion by wind and water when there is an admixture of dirt.

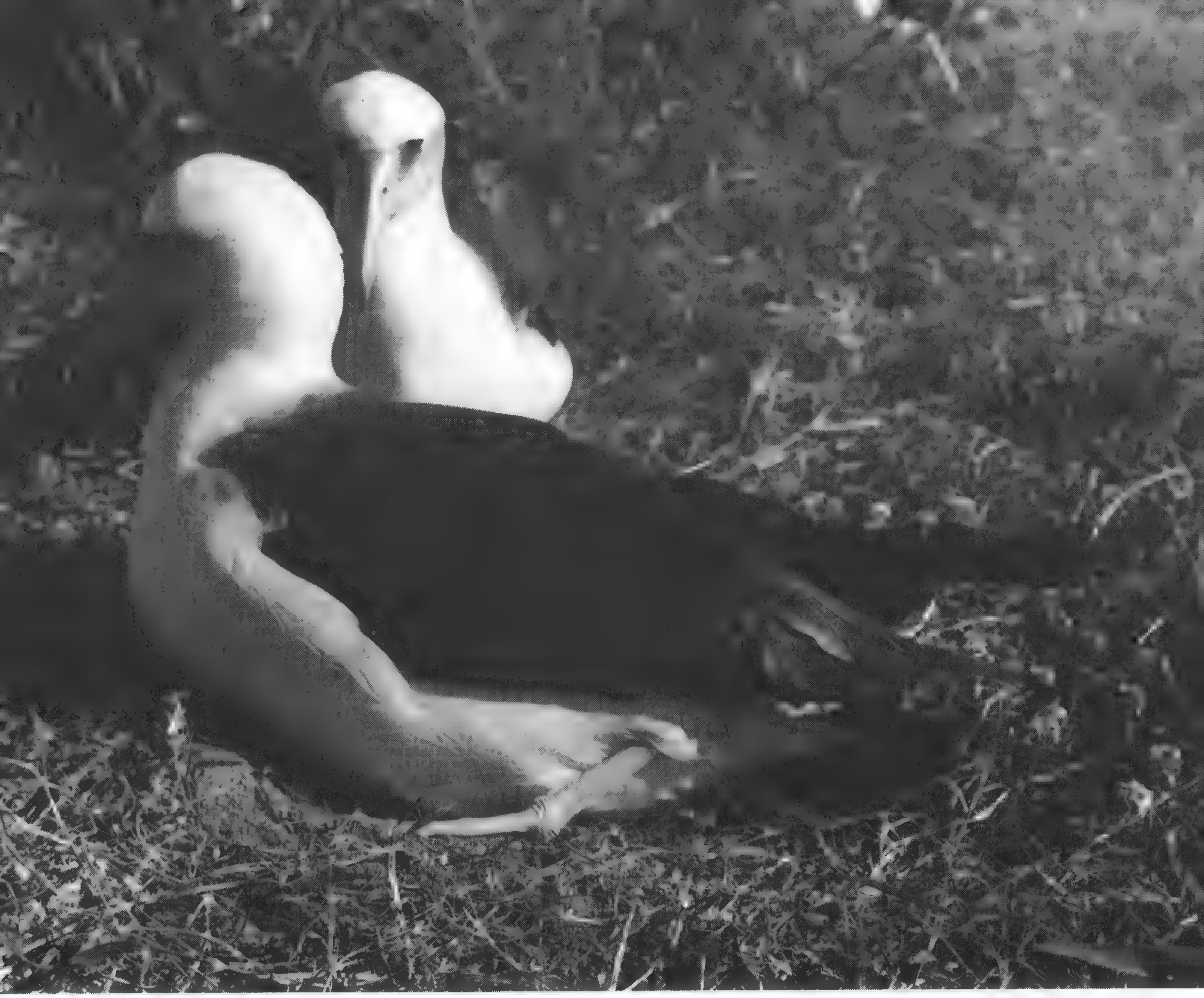


Figure 18. The female prepares a shallow nest scrape for the egg by scratching with one foot and then the other, rotating as she scrapes. The male is not always present.

The diameters of completed nests, including the surrounding "borrow pit" from which the bird scooped the material, range from 34 to 40 inches (Figure 20); the height of the rim is usually less than eight inches but may be as high as 10 inches. Both the diameter and the height depend on the size of the male and how far he can reach with his bill. Once the combined height and horizontal distance exceed his reach, he stops building (Figure 21).

Wind and water, the movements of the incubating bird, and the activities of the exchanging birds tend to destroy the nest. Maintenance by both sexes, though it continues during the incubation period, lessens in the later stages and ceases with hatching. In the first few weeks, the chick's scratching keeps the nest bowl free of debris. Sometimes the vigorous scratching lowers the floor of the bowl so much that the chick is literally in a "well" with the top of its head lower than the ground outside the nest.

Within a month after hatching, the nest as a formed structure disappears, leaving only a barren space with scraps of nest material, the chick, possibly the skeletal remains of last year's chick, and some dried fecal matter.

The incubating birds forcefully defecate beyond the rim of the nest and the chick soon does the same so that as time passes, numerous radiating "spokes" mark the site. Later, lush vegetation grows on these spokes; the ecological succession from sand to vegetation is rapid in albatross colonies on coral islands where the only fertilizer comes from the wastes and decaying bodies of the birds.

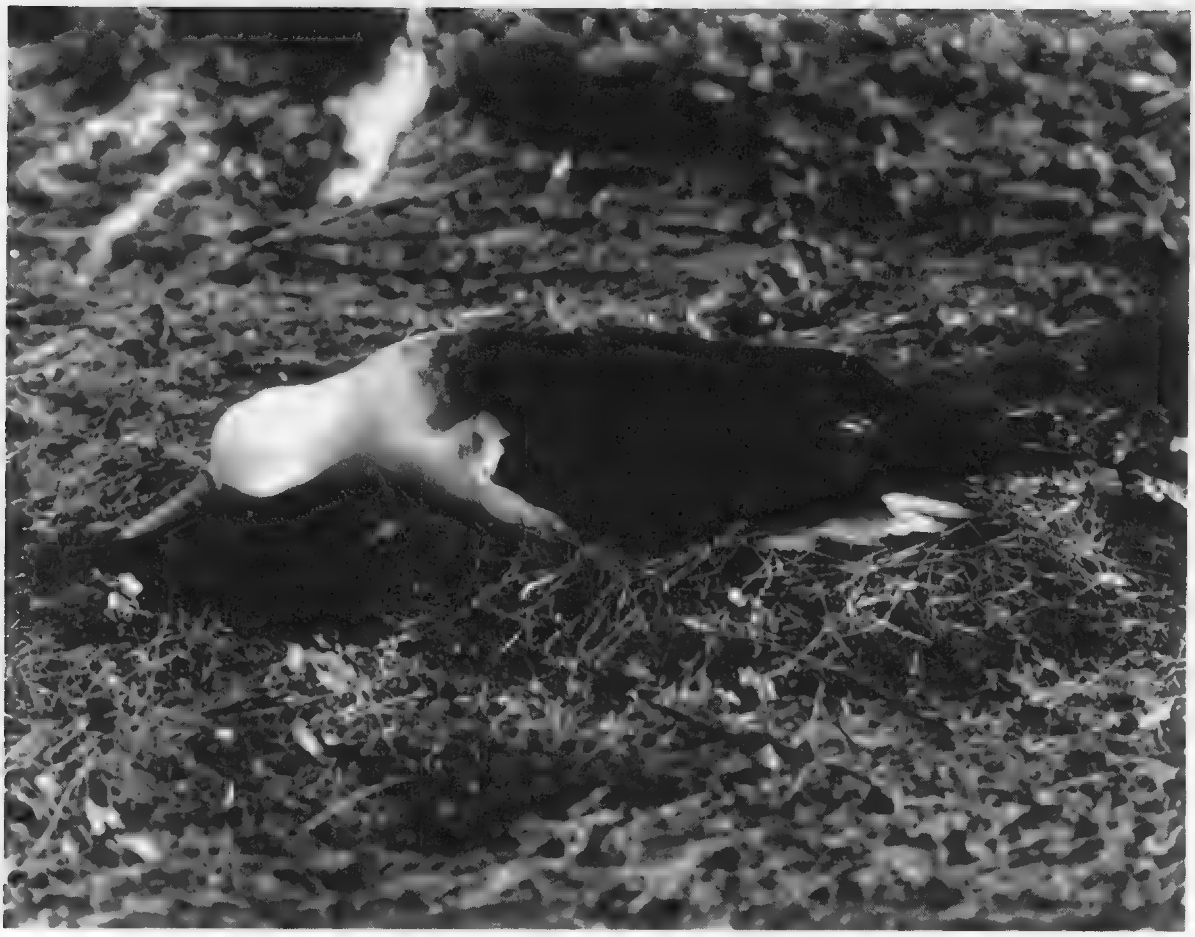
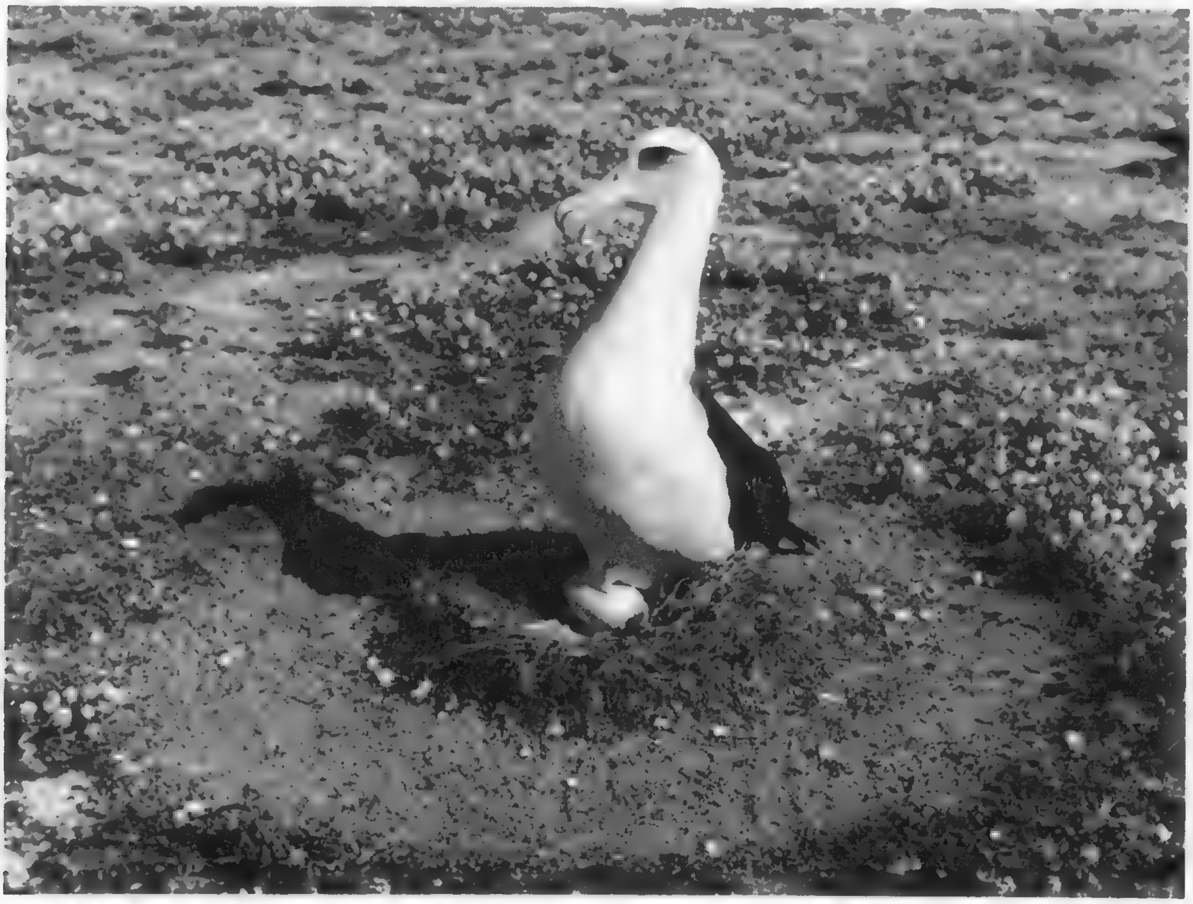


Figure 19 (*above*). During his first span of incubation the male Laysan Albatross completes the nest, dragging in materials from as far as he can reach from the nest.

Figure 20 (*below*). The transfer of materials to the nest may produce a circular, cleared depression — "the moat" — around the nest, especially when there is little loose ground cover.



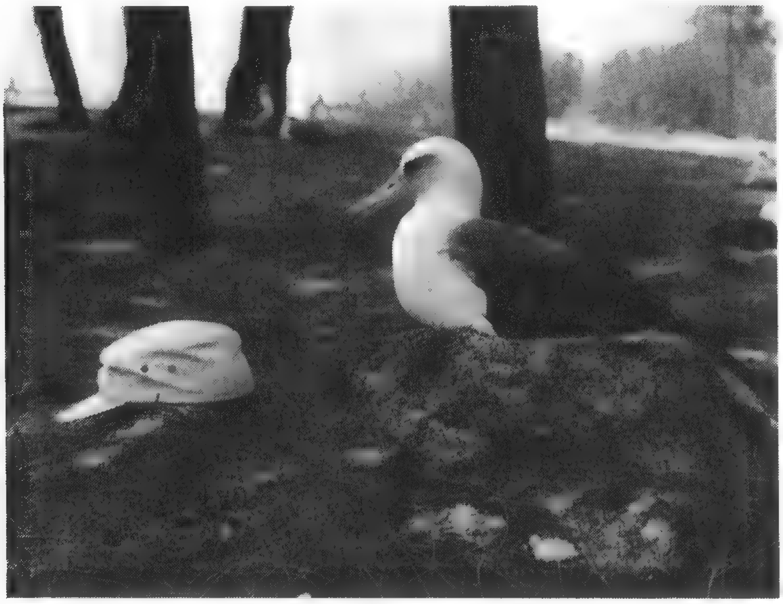


Figure 21. The male ceases building when his bill can no longer reach beyond the sloping base of the nest.

Defense and Nest-site Tenacity

The great persistence of the Laysan Albatross in incubation, shown by the long spans, appears in other ways as well. We know of some males and females that incubated infertile eggs for as long as 108 days and others that brooded the fragments of a broken egg for a week. Adults, and even juveniles, temporarily adopt any exposed egg. Many times, when we lifted an incubating bird from its nest, a bird incubating on an adjacent nest moved over to cover the exposed egg.

We believe that, with some exceptions, the egg, not the nest, furnishes the primary stimulus for incubation and defense of site. Apparently the sight of the egg in a nest is a stronger stimulus than the "feel" of the egg in the pouch.

A Laysan does not leave a nest containing an egg or a chick, and that nest is the only site from which the bird will not move when a person approaches. Females appear to be warier and are more inclined to step aside than males; once picked up, they are more docile. Although the bird may threaten dogs and people from a sitting or standing position, it does not leave. Even raising the bird with a hand or stick to examine the egg will not dislodge the bird. Sorenson (1950a) emphasized this trait in the Royal Albatross and also reported defensive bill thrusts, adding that "Some birds do actually vomit . . . ." after bill rattling and retching.

Bill thrusts are the primary defense of nesting Laysans; retching is infrequent; vomiting is unusual and limited to birds newly returned from the sea. An examination of specimens showed that, after several days on the nest, the digestive tract is empty. Lack (1968:125), who stated that Procellariiformes do not defend against predators, should study albatrosses.

I never saw Laysans defend the egg by covering it with the feet as Murphy (1936) reported for the Yellow-nosed Albatross.

Both male and female Laysan Albatrosses defend the nest and egg against all other albatrosses by threatening with sharp bill-clacking sounds and repeated thrusts of partly opened bills (Figure 22). These acts, though very transitory, are effective. I never saw an albatross even try to take over a nest or egg when the owner was present. Passing albatrosses either ignore the defenders or dodge.

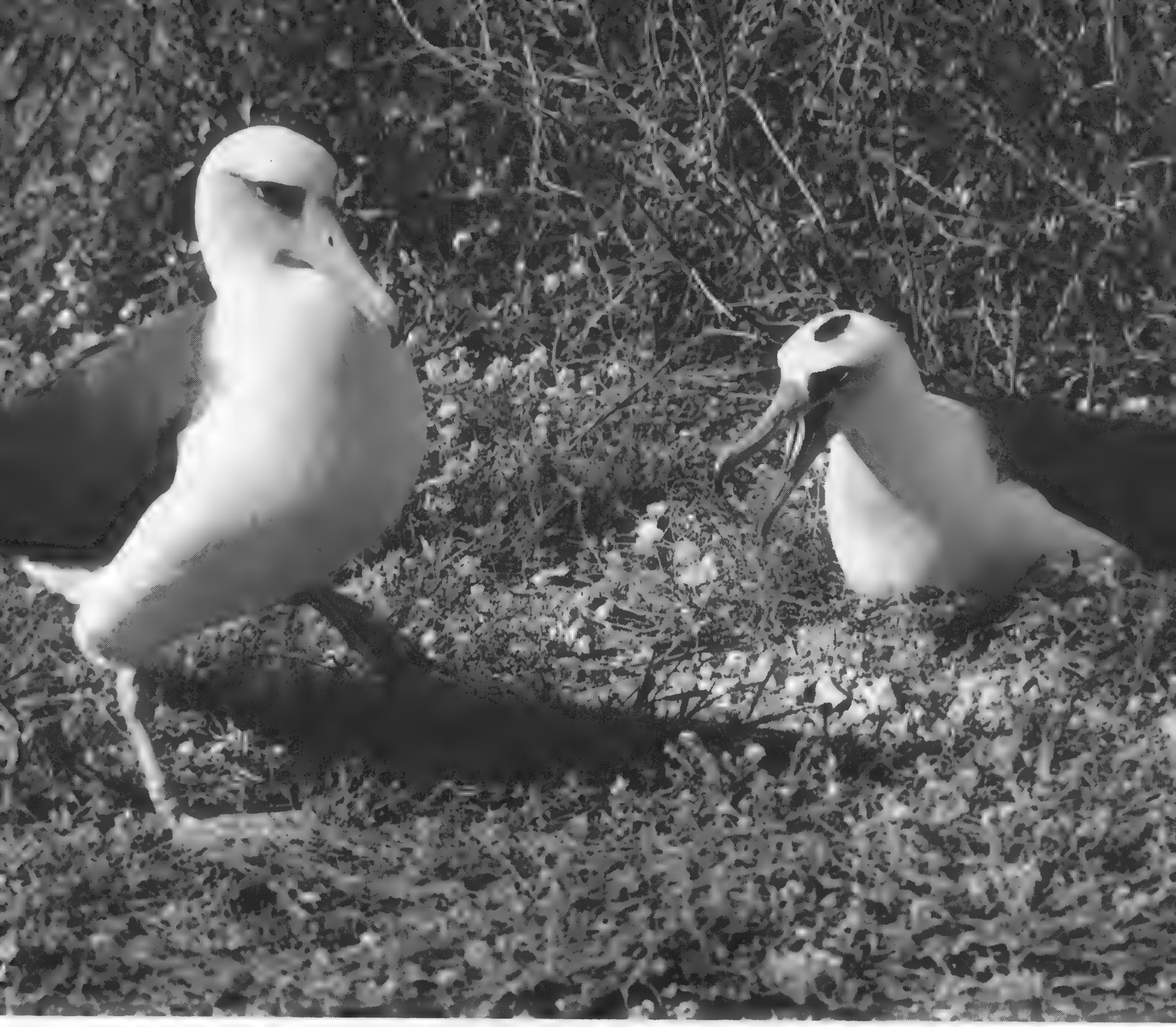


Figure 22. Incubating Laysans of both sexes threaten passing albatrosses with sharp bill-clacking sounds and repeated thrusts of the partly opened bill.

The most vigorous defense of the nest site — by the female, just hours before she lays the egg and shortly thereafter—spaces the nest and prevents later altercations and disruptions. While preparing her scrape for the egg she crouches over the site, with head and neck thrust forward, and attacks any female within reach. The second female, if she is also selecting or defending a site, assumes the same position. Both "growl" and "mutter" and slash at each other with partly opened bills, which may interlock in a tug-of-war (Figures 23 and 24) and leave face, throat, and mouth torn and bleeding. Finally, when one or both retreat an inch or so and they can no longer contact each other with their bills, the conflict ceases.

In most instances, the minimal distance sufficient to separate both members of both pairs is from 32 to 34 inches between the centers of adjacent sites. Since males average larger than females and have a longer reach, the males may resume the battle when they take over. Although either sex defends against either sex, the conflict between two males is sharper and one soon deserts the egg. The distance between Laysan Albatross nests must be great enough to prevent a bird from contacting the birds on adjacent nests (Figure 25). According to "Fisher's Law," the shortest distance between adjacent nests must be greater than the combined lengths of the heads and necks of the two largest members of the two pairs.

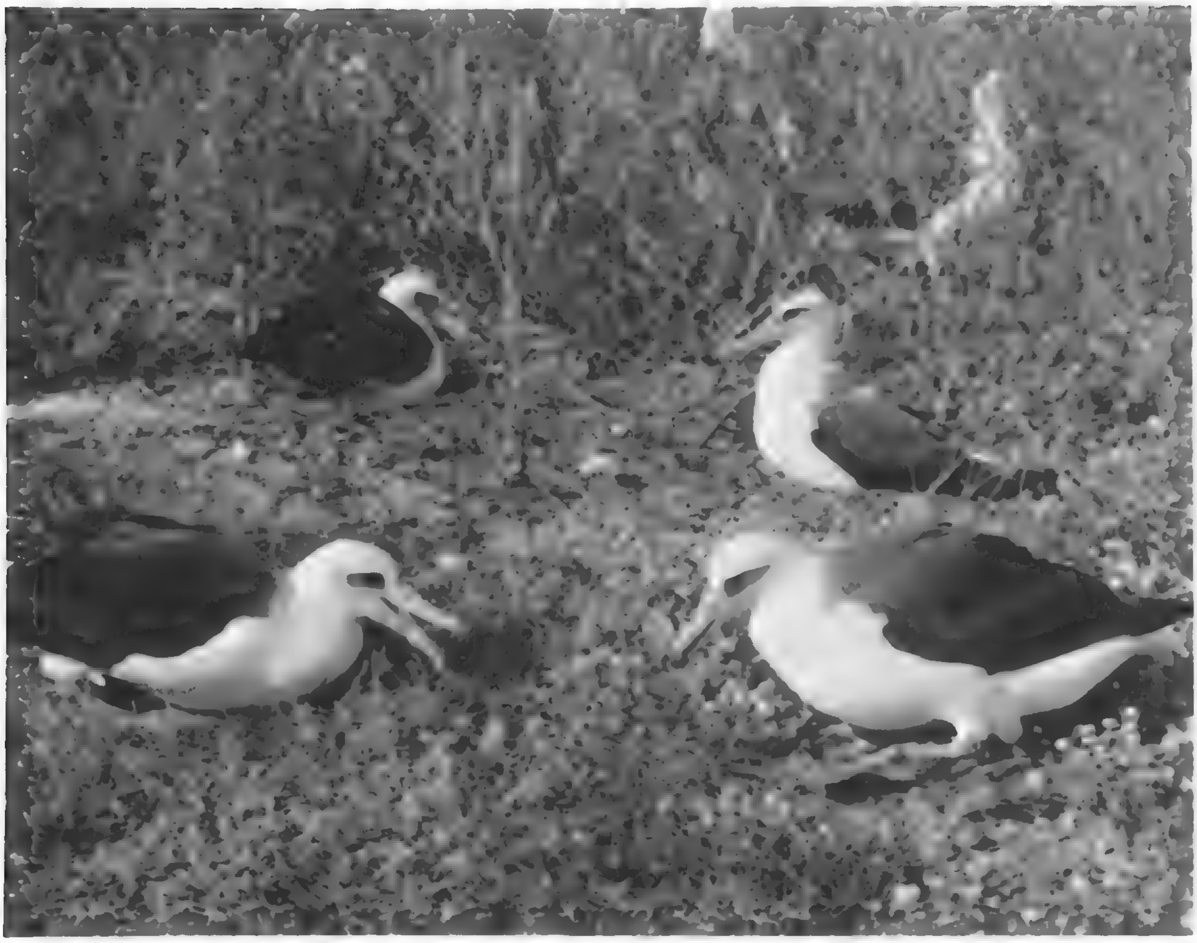
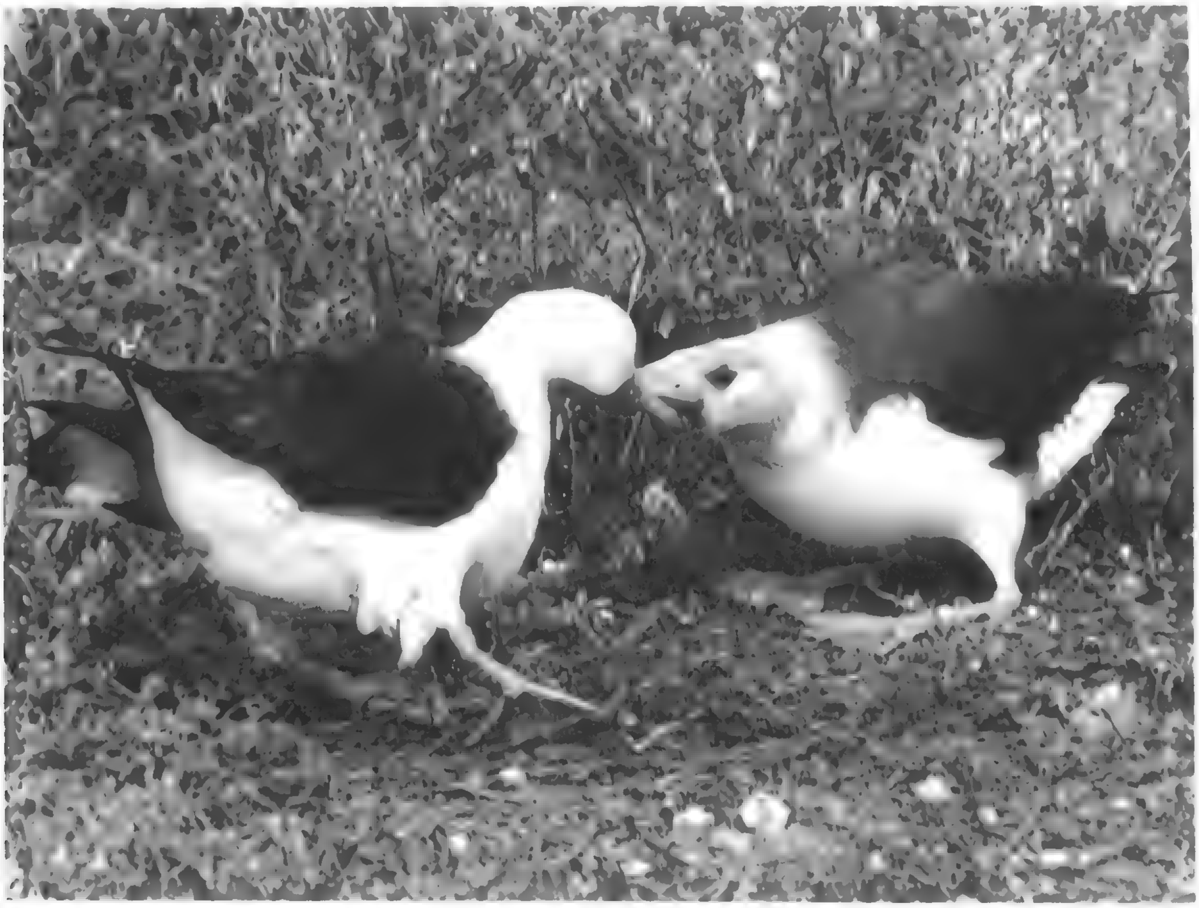


Figure 23 (*above*). Females space their nests by attacking any other female within reach. These battles result in an inch-by-inch retreat by one female.

Figure 24 (*below*). Sometimes the spacing squabbles become bloody tugs-of-war when the females clasp each other's bills.



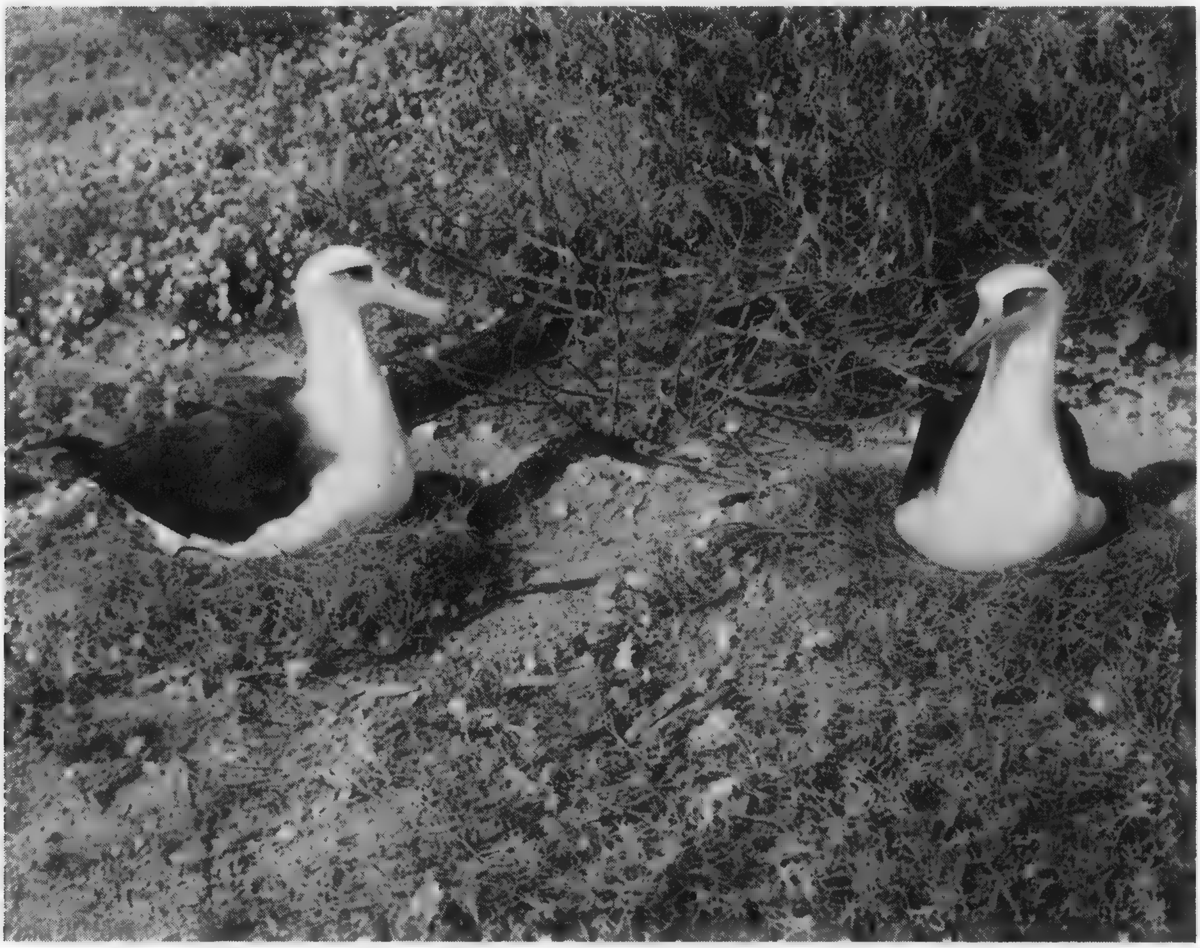


Figure 25. The necessary minimal distance between nests is shown by the two incubating males; they were mates of the females shown in Figure 23.

However, in brushy or weedy areas the nests may be closer, only 15 or 20 inches apart, if there is a screen of vegetation between them. Eventually, this may lead to trouble, as noted later, when the activities of the incubating birds wear down the screen.

The Laysan's behavior in stormy weather shows the site-tenacity in this species. Nesting birds desert only under the worst conditions and only after they have tried repeatedly to stay on the egg. In bad storms, they face the wind, retract the neck and head, and squat as low as possible, retaining this position even when the sand piles up around them and covers all but the head and neck. In severe rainstorms, the rain and wind-driven sand separates the feathers on breast and neck, soaks the albatrosses with water, and crusts them with sand. The birds leave only when the wind actually blows them off or the water washes them off, and they try over and over again to return. If a bird can stay on the nest, it does, even though it cannot maneuver the egg into the pouch. Since the bird does not lift the egg or roll it onto the invading sand, the egg is covered and lost.

Earlier I described how birds that try to open the pouch when facing the wind are tipped backward off the nest. The strong winds, besides throwing the bird off balance, flatten the feathers over the pouch so that the bird cannot open it. Some Laysans turn their backs to the wind, raise up, secure the egg in the pouch, lower themselves, and turn slowly — 10 or 15 degrees at a time — until they again face the wind.

The problem of the egg dropping from the pouch is present every time the bird stands to rest, defecate, or shake off the sand during a storm. Sometimes the bird, in struggling to free itself from the sand that imprisons it, buries the egg. Since a covered egg is neither a visual nor a tactile stimulus, the bird deserts.

Unquestionably, storms "bother" the incubating birds. They cower on their nests and are more prone than usual to clack their bills and snap at passing birds or people. Even birds relieved of nest duty seek shelter behind clumps of weeds or brush or coral hillocks rather than fly out to sea.

Exchanges at the Nest

Nest-relief ceremonies, with few exceptions, take place only between members of a pair. Occasionally, when its mate is long overdue, an incubating bird may exchange with another male or female. The exchange usually occurs in daylight, but once in a while by moonlight or under a street lamp. Three-fourths of the exchanges take place between morning twilight and noon.

The incubating birds recognize their mates by sight up to 20 or 30 feet away. We know this because the returning mates are silent until a few feet from the nest. They may also recognize them by sound at this distance, although it is impossible to separate the reactions to sight and sound. The recognition of voice is evident when a sleeping bird is awakened by its mate standing alongside or a wide-awake bird is unaware of its mate approaching from the "blind side" until it hears the voice. We have no evidence of recognition between a bird on the ground and its mate in the air.

We could not verify the observation of Bartholomew and Howell (1964: 554) that a normal exchange might occur if a nest in a colony is moved several yards. We moved nests within the colony and noted only exchanges between members of second or third pairs that temporarily claimed the egg after the original owner deserted. In similar experiments, with nests several yards apart and on the margin of the colony, the members of the original pairs exchanged on three of 20 nests. We believe that, in the initial stages of exchange, location of nest is the primary focus of the returning bird and that recognition of mate is secondary.

The incubating member may show the first sign of recognition by rising and immediately, or simultaneously, *eh ehing*. Both birds *eh eh* until their extended bills touch. The incubating bird "looks at the egg" and *eh ehs* (Figure 26). The relieving bird looks at the egg, *eh ehs,* and may preen briefly the head and neck of the mate on the nest. Shortly thereafter, the returning bird rests with its breast on the rim of the nest, either alongside its mate, head by head (Figure 27), or head toward the rear and overlapping that of its mate. Either bird may give single, soft bill claps during these activities.

After resting a few minutes, they start mutual preening. From time to time, the relieving bird rises, circles its mate, and perhaps rests on the opposite side of the nest. The resting and mutual preening may continue for minutes or hours before the relieving bird actually attempts to cover the egg. It frequently tries to put its bill across the back of the neck or shoulders of the incubating bird, which may fend off the action several times before permitting it. Males, more than females, perform the bill-over-the-neck in their repertoire of exchange behaviors. The Short-tailed Albatross, *Diomedea albatrus* (Fujisawa, 1967:37, photo 20) apparently has the same behavior in its exchange.

The bill-over-the-neck action is so similar to that of a male trying to gain acquiescence for copulation that we believe it indicates the dominance of the performer and the recognition of that dominance by the receiver. This increases submissiveness and thereby eases the exchange.

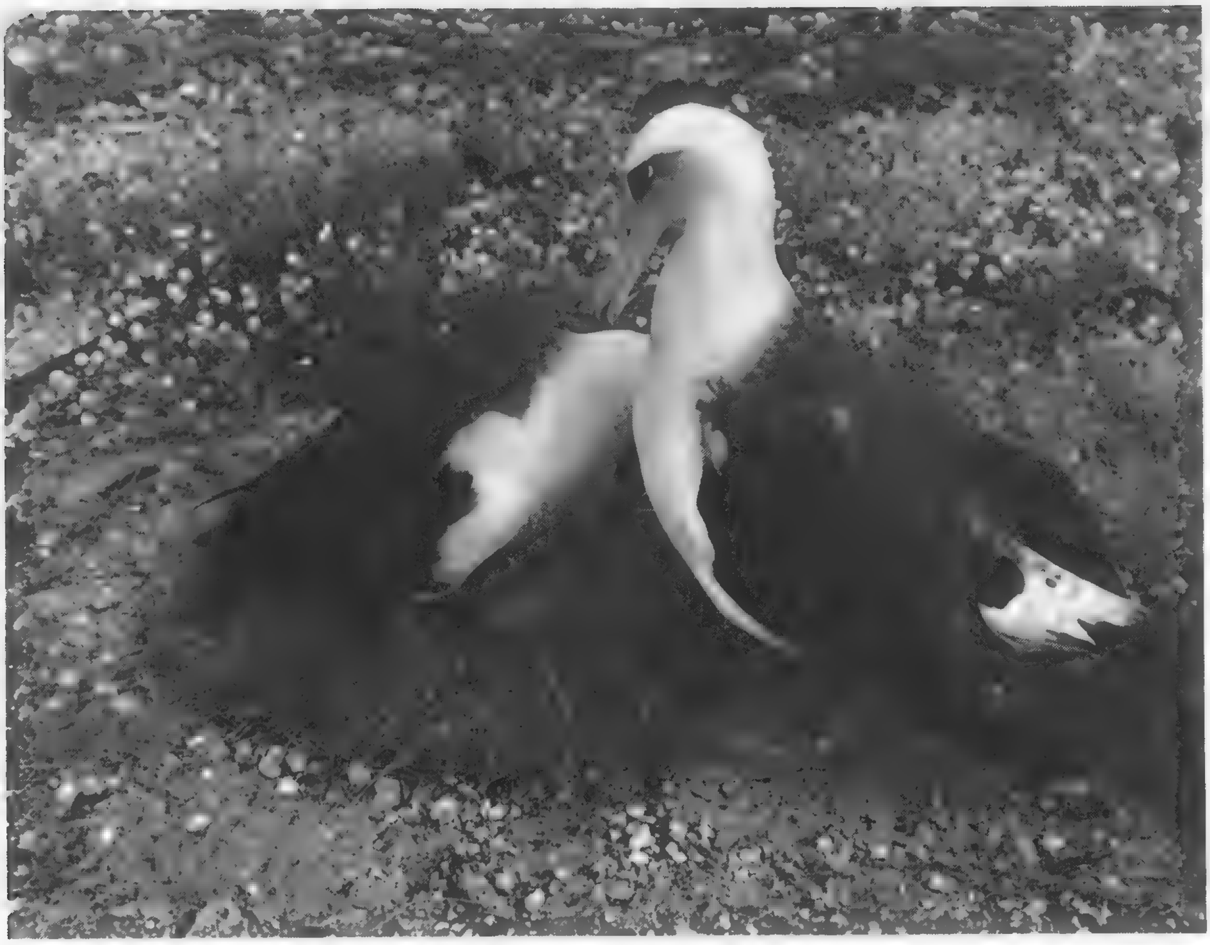
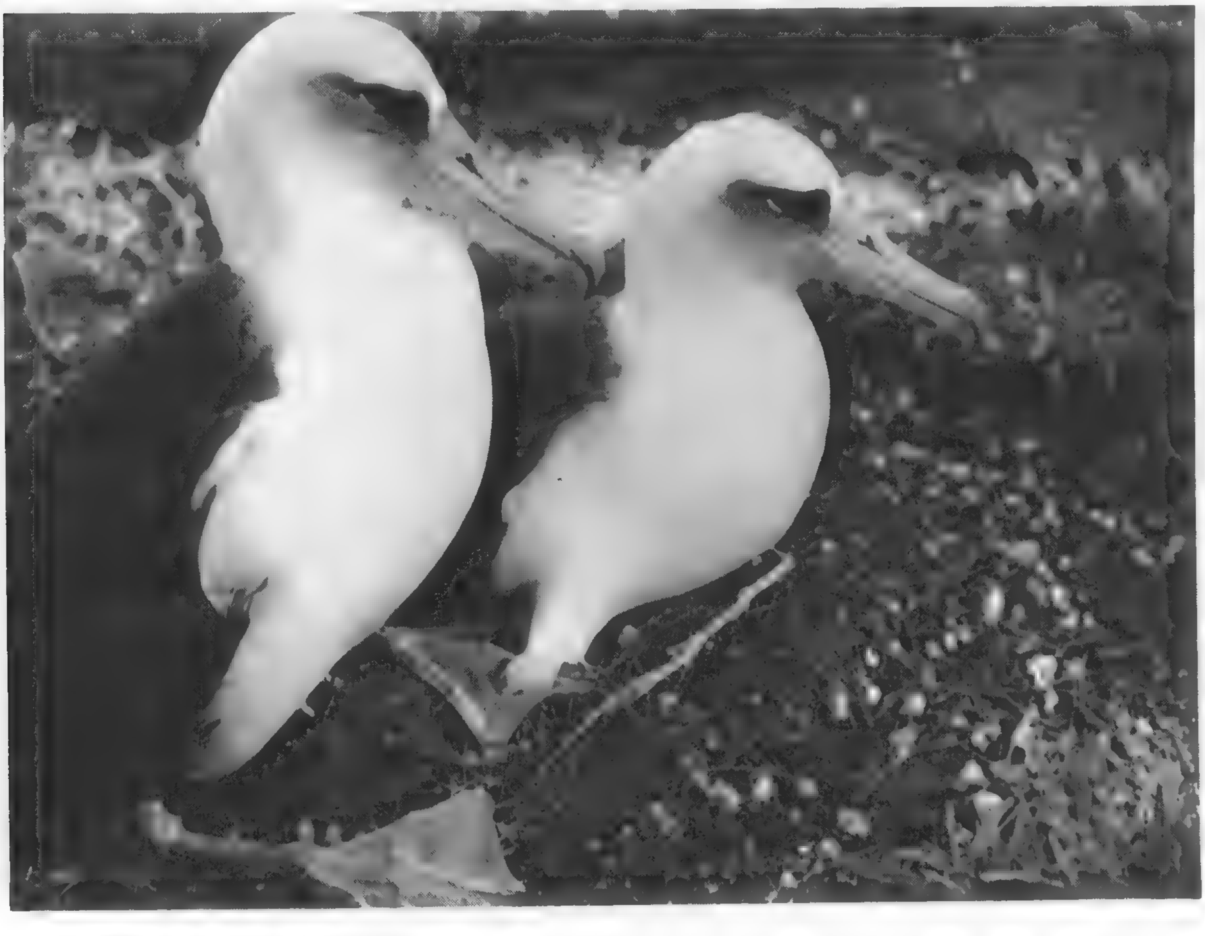


Figure 26 (*above*). When a bird returns to relieve its mate, the incubating bird rises to expose its egg and to "talk to it."

Figure 27 (*below*). The relieving Laysan often rests from its activities and sits on the edge of the nest.



Seldom does the relieving bird toss nest materials. We think it occurs mostly in prolonged nest-relief ceremonies when the relieving bird must use its whole repertoire of signals to induce the incubating bird to permit the exchange. Eventually, when its mate stands, the relieving bird looks at the egg and tries to keep its head and neck in the nest bowl, pushing its shoulder or breast against the mate (Figure 28). Seldom is the first or second attempt successful. Rarely, the relieving bird tries to push its mate off the nest by lifting its tail and backing up.

The pair may again sink onto their breasts for more mutual preening (Figure 29). Soon this gives way to more slow circling and *eh ehing* by the reliever which eventually succeeds in keeping its head in the nest and pushing its mate onto the rim. There the mate rests while the reliever fits the egg into its pouch. Once the egg is secure, the incubating bird *eh ehs* to it.

Sometimes the relieving bird pushes so vigorously that it churns up dirt and sand and almost rolls its "heavy-setting" mate out of the nest. Then the relieved bird, even before steadying itself, may bend toward the egg and *eh eh*.

The relieved bird may still be hesitant to depart. After resting briefly on the rim or within a couple of feet of the nest, it may preen, arrange its rumpled feathers, lift the feathers on its breast with its bill, or toss nest material in any direction. Males more often perform the preening and tossing, which probably are displacement activities.

The time between the exchange and going to sea varies, depending on the weather and, presumably, the bird's internal state. Good weather shortens the time; storms may lengthen it to 24 hours or more. Most relieved birds depart within an hour or so.

We never saw a relieved bird fly back over the nest or land to preen its mate as Sorenson (1950a:16) noted in the Royal Albatross.

A few relieved males or females, reluctant to leave, sometimes move onto deserted eggs nearby and incubate them for several days. This disrupts the timing at their own nest and is detrimental to the colony as a whole. In three instances, such birds sat for four, 13, and 17 days, so delaying their return to the sea for feeding that they were late to begin their next span. When they finally returned to their own nests, their mates had deserted.

The above description of the exchange is an average picture. For specific details of one exchange I quote from my field notes of 15 December 1962:

> Male on nest; female approaches slowly and touches breast and head of male who rises to show egg; female nuzzles head and breast of male; male rises and talks to egg (*eh eh*); female puts bill in nest and touches egg; she rises and goes through the motions of getting egg into pouch; she stands erect and nibbles bill of male; pecks gently at male's head and shoulder; male *eh ehs*, but does not rise; female sits down face to face with male, bills side by side; male rises; female pushing on side with breast; male recovers and sits on egg; she now pushes her breast against his side and gets one foot in the nest; female touches egg with bill and continues to push male, but now with her side, still with one foot in nest; both look at egg exposed between them; female sits down on rim, male on opposite rim; male pushes back onto egg, then rises and looks at egg; she now more vigorous with pushes; male draws weed stems in toward nest; female stands and preens very briefly, then nuzzles side of male's neck; she sits facing male; she stands and preens; male draws in more nest materials; he rises and walks off nest; female stands over egg, touches it with bill, and talks to it; male talks to egg and sits down on nest rim, side by side with female; male warns dancing pair three feet away; he walks around nest; male *eh ehs* and tries to push female off; now she pulls nest material, as does male; female rises, looks and talks to egg; male *eh ehs* to egg exposed when female rose; he warns dancers again and walks two feet from nest; female stands; male throws nest materials; she rises and talks to egg; male comes and talks to exposed egg; he leaves.

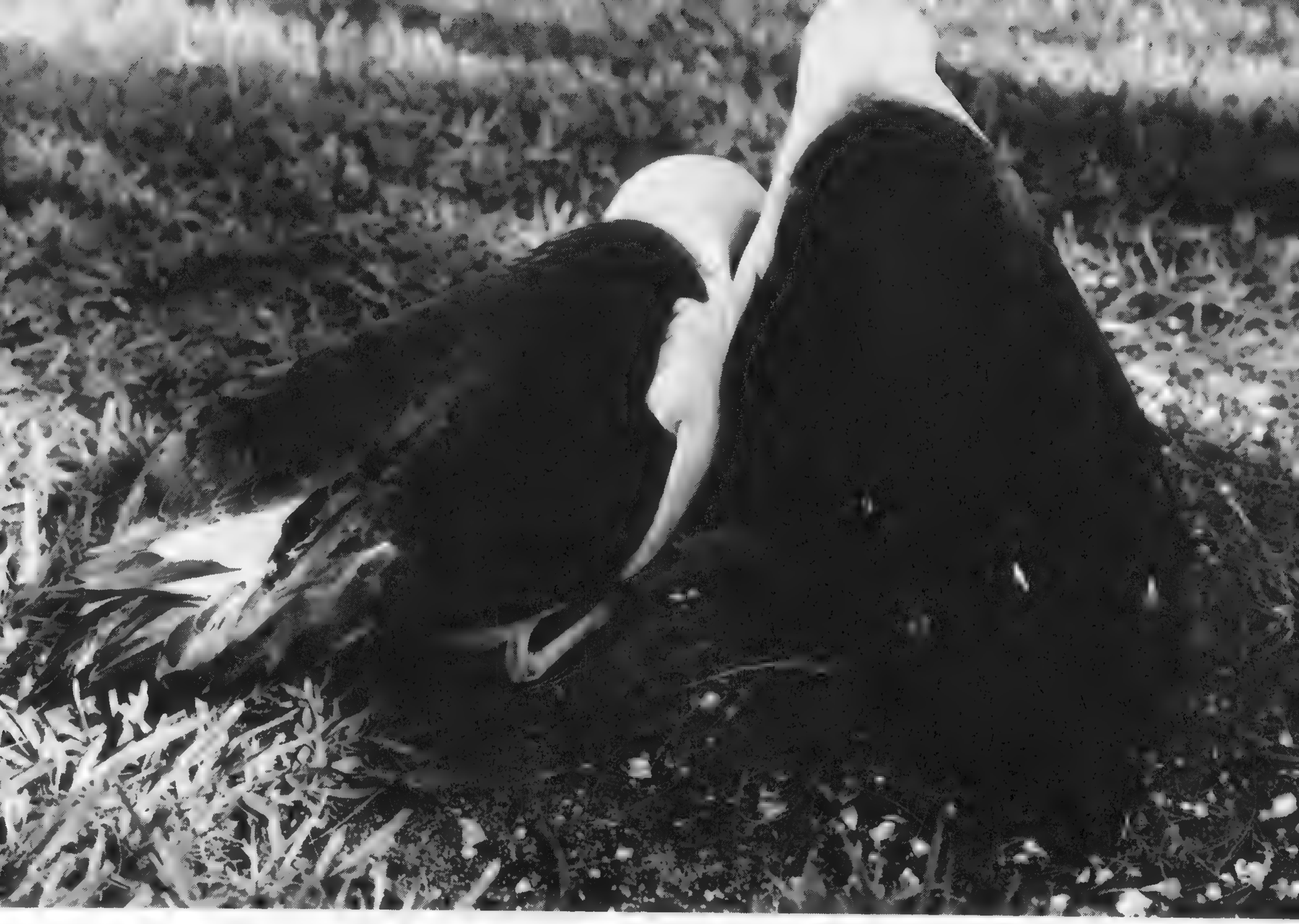
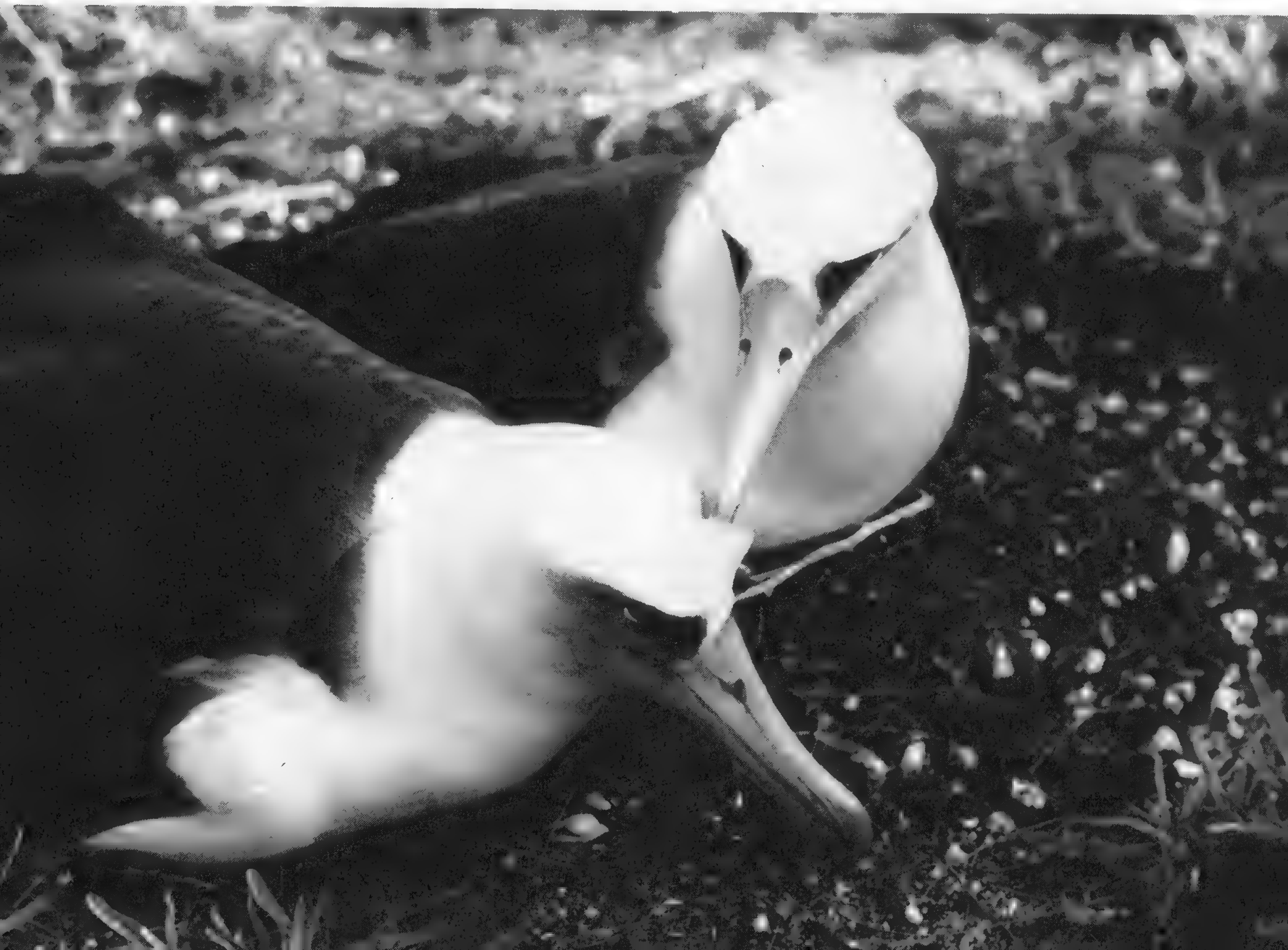


Figure 28 (*above*). The setting bird, reluctant to leave, is eventually pushed out of the nest by the relieving bird which manages to get its bill and one foot in the nest bowl and forces its way onto the egg.

Figure 29 (*below*). Mutual preening occurs before, during, and sometimes after the nest-relief ceremonies.



One example demonstrates the occasional deviation from the normal sequence of span and exchange: An experienced pair began nesting. After three days the female deserted and a seven-year-old unpaired female moved in. The male returned, exchanged with the strange female, and remained for an average span — until relieved by his original mate who, in turn, was relieved by the strange female. From then on, the two females shared the spans normal for the female. The male's spans were approximately average in duration; the change did not disturb his cycle and the egg hatched. Two years later, the young female nested successfully with her own mate. Kenyon *et al.* (1958:34) may have been describing a similar instance when he wrote of a bird incubating ". . . with the help of a new mate." I do not believe they ever obtain "new mates" that rapidly. Pair formation and mating are a slow process in Laysans.

We offer this explanation: The experienced female was a chronic deserter; she had deserted previously and she deserted later, three times in seven years. The young female, though sexually mature, was unmated and a stranger on this nest. Both females, therefore, had less than a normal drive to incubate, making nest-relief easy, yet both had enough drive to keep them on the nest for part of the span.

The difficulty of nest-relief seems to lessen as incubation continues. This is surprising because the spans become shorter and the attentiveness to the egg, as in most species, greater. A study of the weights of incubating birds (H. I. Fisher, 1967) revealed that each sex regains the weight lost in the first long span before it returns to the nest for its next span; but neither sex regains, before returning, the weight lost in subsequent shorter spans. Therefore, despite the facts that desertions decrease and the bird's attentiveness to the egg increases, the stimulation by hunger increases even more. The stimulus to eat and drink is stronger than the stimulus to sit on the egg, the bird is more willing to leave, and exchanges are less difficult in the later stages of incubation. In addition, the urge to incubate may weaken as the period progresses.

The exchange-of-duties ceremony at the nest increases the chances of successful reproduction by: 1, insuring that the egg is never left uncovered, thus preventing other albatrosses from incubating it temporarily; 2, "fixing" the incubating bird on the egg until relieved, thus preventing loss by chilling; 3, reducing conflict at the nest, and thus preventing breakage; and 4, preventing a bird, other than the mate, from incubating. This last is most important. The members of a pair have a fixed cycle of duty and relief, initiated on the day the female laid the egg. Any interruption by a bird on a different cycle, a different part of the cycle, or no cycle, increases the chances of desertion.

The exchange rites firm the pair-bond of these albatrosses which meet so infrequently (H. I. Fisher and M. L. Fisher, 1969).

The Taking Over of the Egg

The fact that the sight of an egg stimulates brooding in every Laysan, regardless of age or breeding status, is a significant benefit to the species. It may also be detrimental. Non-breeding birds immediately try to cover any exposed egg and, if the bird is a juvenile, may break it. Should either or both the owners return while the intruder is on the egg, the owner takes offensive action. If the intruder defends desultorily, the owner retires a short distance. Female intruders seem to defend against both male and female owners; male intruders seem less inclined to defend against male owners, probably because of the latter's dominance. Since unpaired birds seldom exchange and since usurpers are not prepared physiologically for sustained incubation, the egg is again exposed. If the owner departs before the intruder loses interest, the nest is unsuccessful.

We have many instances of three, four, or five birds successively incubating the same egg, and occasional instances of another female laying a second egg in a nest (H. I. Fisher, 1968). The birds incubating one egg may include the original pair, perhaps a pair of young birds, or one to three individuals not known to breed in the study plot. All of these nests fail.

In December 1968, I "built" a nest and placed a deserted egg in it. In five hours, at least six different birds "incubated" the egg.

Although this taking over occurs frequently in the colony, two factors work against excessive nest loss. Normally, the egg is not exposed except during the nest-relief ceremonies when both parents stand over it. Second, the majority of wandering juveniles do not arrive until incubation is over (H. I. Fisher and M. L. Fisher, 1969). Former breeders and older juveniles present during the incubation season are usually psychologically attached to a station. Hence, only the eggs close to their stations are in danger.

Obviously, the inclination to incubate any egg must have survival value exceeding its detrimental value to the species or it would not continue as a behavioral trait.

Behavior of Deserters

Males and females that abandon eggs return to the colony from time to time during that breeding season. Those that desert early come back several times during the incubation period, less frequently from hatching to March or April, and seldom later. Our observations differed from those on the Royal Albatross by Richdale (1950:53) who believed that birds deserting eggs did not return that season, but that birds losing or breaking their eggs ". . . loiter around the vicinity of the nest-site for at least two and sometimes three weeks before disappearing for that season."

The members of the pair of deserting albatrosses return and depart separately. Any meeting at the male's station seems to be accidental and without pattern. However, the first member deserting may return after an absence approximating a normal incubation span. Since its mate, having already returned to a cold egg or empty nest, is most often gone, the cycle is broken in both birds.

The return of the deserters to the colony probably serves two major functions: The male, by his periodic presence throughout the main territory-seeking season of the younger males, maintains the property rights of his station, which, in turn, may prevent conflicts the next season. Such conflicts might reduce the chances for successful breeding by the owner and the younger males. In one sense, this tendency to return is more beneficial to other individuals and hence to the species as a whole than to the individual male. It may well support some of the views of Wynne-Edwards (1959, 1965) on the importance of group behavior, Lack (1968) to the contrary.

The chance meetings of the pair at the home station, usually for only a day or so, must reinforce the pair-bond. The two rest side by side, often closely pressed together, on the nest site or nearby, but always on the home station. They mutually preen for hours; they may perform incomplete courtship dances, sometimes over the abandoned egg. Richdale (1950) indicated this same "reversion" to the "usual love-habits of the pre-egg stage."

When one member of the pair is alone, it sometimes starts to build a rim around the oftentimes misplaced egg, forms another shallow nest bowl, or dances with nearby birds. Males do this more often than females and stay closer to the home station; females may wander about and dance with solitary males over a hundred-yard circle.

On the time basis alone, one-sixth of the deaths of mature birds should occur during the two-month incubation period, and the rigors of nest duty and weather may well increase this rate. Desertion is often due to the death of a mate. The behavior of deserters may, therefore, be a prelude to seeking a new mate. The male stays on the home station and dances with passing females because he must be there to attract one. The female wanders among and associates with other land-holding males because, with the death of her mate, she has lost her rights to a home station and can gain new rights only by pairing with a territory-holding male (H. I. Fisher, MS).

Despite their wanderings, the members of a pair always go first to the home station and periodically return to it. If the mate happens to be there at the same time, the old pair-bond is strengthened and any temporary liaisons broken.

Looking at the Egg

Both incubating birds look at the egg. Seldom does a bird rise, even in storms, without bending forward to look at the egg and perhaps touch it with the bill. The bird looks at the egg when it rises to rest a few minutes or to stretch a wing or leg, when people approach, when somebody lifts it off the nest, when the mate approaches prior to the exchange ceremony, and when the relieving bird is adjusting the egg in its pouch.

Since the dense heavy feathers and skin form such a close fitting "sac," the egg may stay in the pouch when the bird rises. Looking at the egg may be one means of reducing the possibilities of displacing or breaking it. However, looking at the egg is so important in the nest-relief ritual that we believe it also incites a "desire" to incubate in the relieving bird. Perhaps the reason for the evolution and retention of this habit is to reinforce the internal stimulation to incubate.

Talking to the Egg

Frequently, though not always, "talking to the egg" accompanies looking at the egg. Holding the bill next to the egg, the brooding bird gives a series, usually two to four, *eh ehs* (Figure 30). These sounds, though heard throughout incubation, are more frequent in its later stages and are uttered by single birds or members of a pair when the egg is uncovered. As far as the human ear can tell, they are identical to sounds given in many other contexts.

Talking to the egg may be the first step in establishing recognition of the parent's voice in the unhatched chick — a form of early learning or imprinting. Driver (1960) described similar imprinting of sounds on duck embryos, and Gottlieb (1971) discussed in depth the possibility of similar prenatal determinants of perception in chicks and ducklings.

Although we have no detailed studies of sounds produced by the chick before it hatches, we do know it may *peep* two or three days before pipping. The *peep* in the egg sounds identical to the *peep* given later in food-begging. I expect the parent learns to recognize the chick's *peep* about the time the chick recognizes the parent's *eh eh*.

Such early development of recognition is most desirable in altricial, colonial nesting species where the young are left alone during a long fledgling period and may move from the nest at a relatively early age.

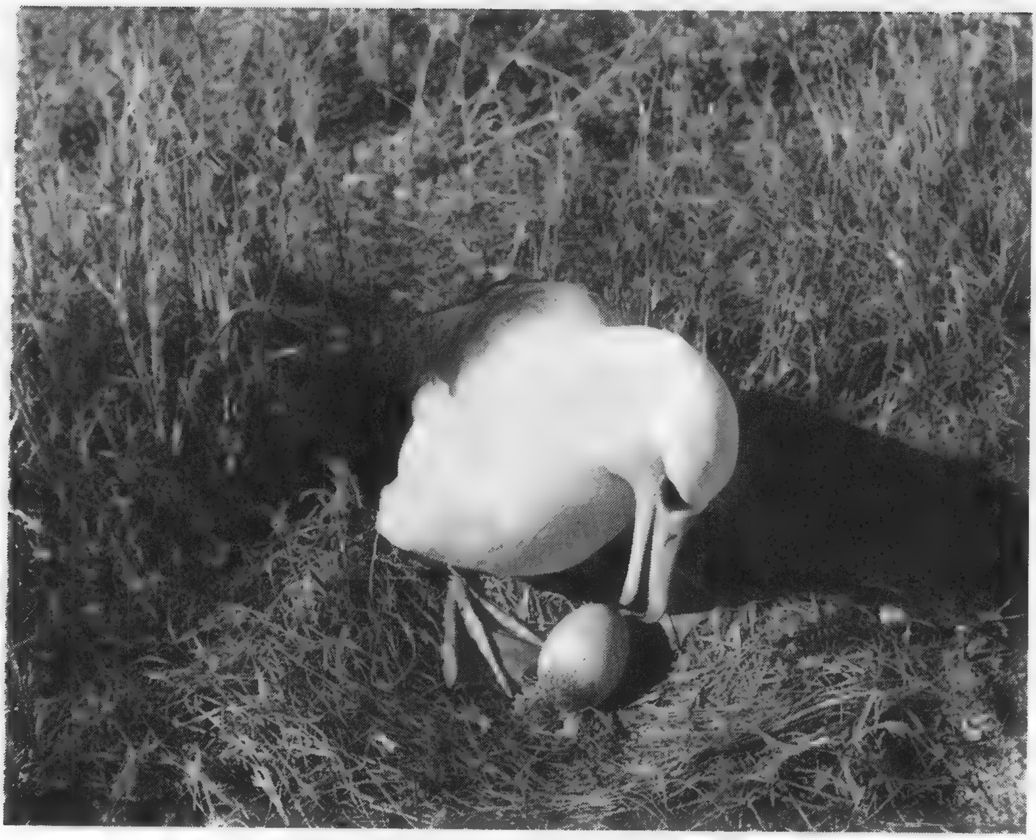


Figure 30. Males and females may rise from the egg and "talk to it" by uttering a series of *eh eh ehs*. The sounds are made more frequently during the later stages of incubation.

Mild Alarm Note

When an intruder other than a strange albatross enters the edge of the nesting colony, the nearest birds clack their bills softly, once or twice, and this reaction spreads to birds within 20 or 30 yards. If the intruder stands motionless, the bill clacking ceases; if he proceeds, the clacking moves ahead of him and dies out behind. He is encircled by birds aware of his presence, direction, and rate of advance even on the darkest nights when the behavior is most frequent.

Should the intruder pick up or molest a bird, the single soft clacks change to hard, rapidly repeated clacks of threat to a recognized danger.

We interpret the soft clacks as alarm signals of low intensity, alerting the sleeping birds, which cannot see the intruder, to the presence of potential danger.

According to Boudreau (1968:28, 40) the Laysan and Black-footed Albatrosses ". . . emit no true alarm sound under any circumstances" and "I have never yet elicited a valid alarm sound from any of the different albatrosses . . . I have studied." I am not certain he studied all the sounds of nesting albatrosses.

Soft Click

Undisturbed birds, incubating and apparently sleeping with eyes closed, make a soft click, audible to the human ear for only a few feet. Many minutes may pass between these single clicks. Since we saw no motion of a bill simultaneously with a click, and no behaviorial reaction in other birds, we could not determine its origin or significance.

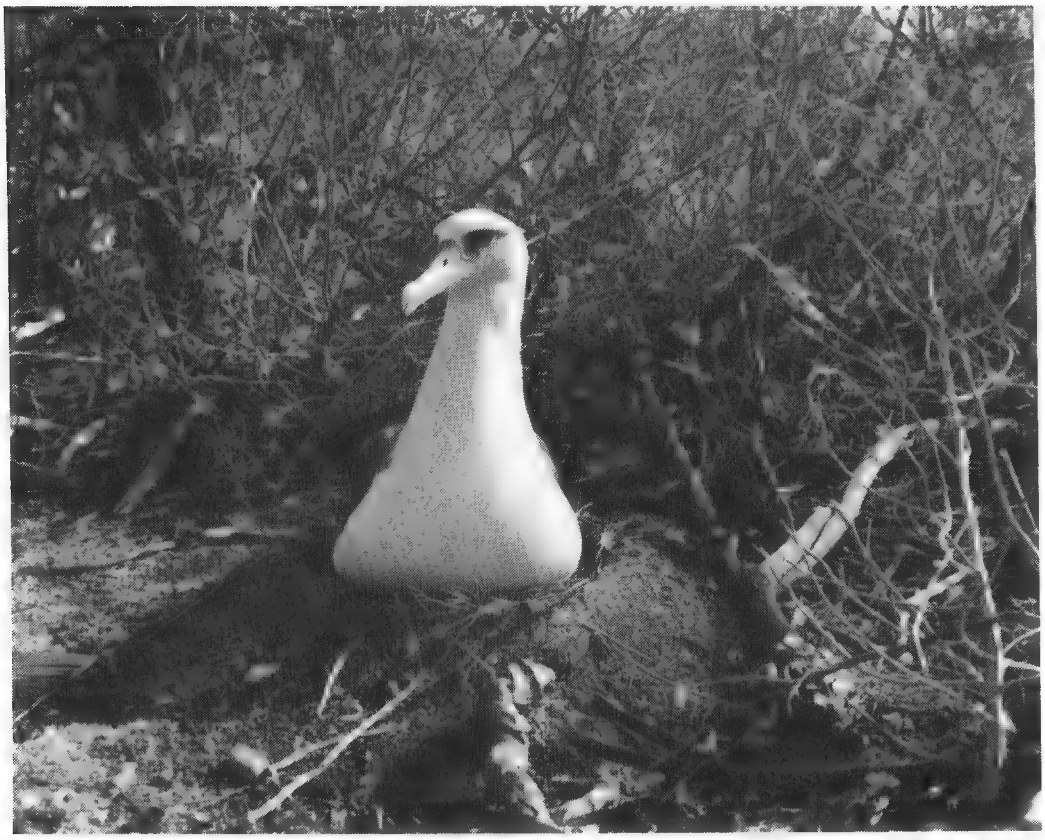


Figure 31. Incubating Laysans often destroy all vegetation within reach, thereby keeping the nest site accessible year after year.

Nonsense Behavior

For the want of a better term, we use "nonsense" to describe a behavior that seems to have no purpose. Perhaps nonsense applies to the following behavior just as well as it does to certain behaviors in migration and navigation.

A nonsense behavior, common to all incubating Laysan Albatrosses, is the tearing up of anything within reach — human debris such as clothing, toys, or newspapers, and any vegetation, even woody plant stems a half inch or more in diameter. Some birds even try their bills on steel cables. They swallow some of the scraps and put some in the nest. J. Fisher (1952:431) noted similar behavior in the Atlantic Fulmar, but offered no explanation.

The local residents believe that the birds tear things up out of "boredom." On the positive side, the birds, by tearing up all vegetation within reach each season and preventing woody plants from encroaching on the site (Figures 31 and 32), may be able to hold the same site for the length of the pair-bond. Brushy growth, if not controlled, becomes impenetrable for albatrosses, as has happened in certain areas on Midway and much of Kure and Lisianski Atolls. On the negative side, the removal of all vegetation around the nest often eliminates the protective screen between nests that were too close together to start with. Conflicts arise and one or both nests fail.

The Guard Phase

In the Southern Hemisphere, the guard phase protects the eggs and young of albatrosses from predatory birds, notably the Skua (*Stercorarius skua*). In the Northern Hemisphere, the guard phase seems to be a relic of this behavior,

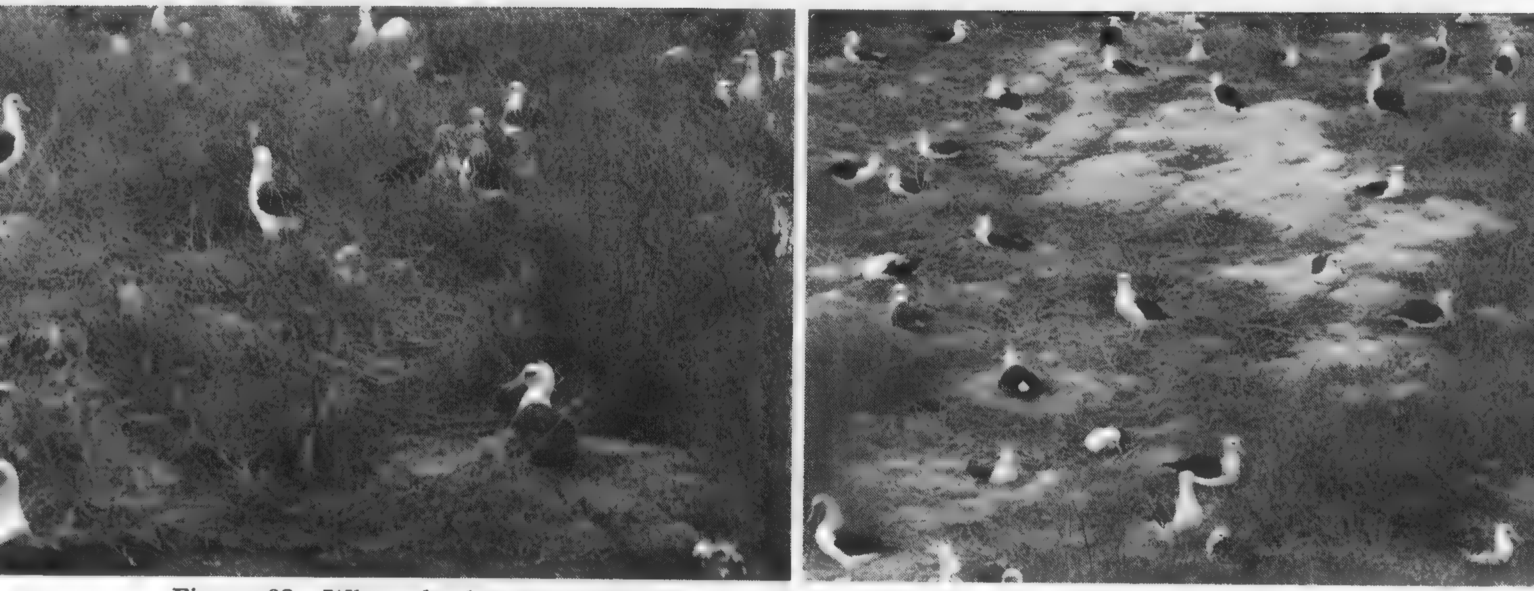


Figure 32. When the breeding birds first return in November, the colony grounds may be covered with weedy growths developed after the birds departed the preceding July (*left*), but the vegetation is soon flattened by birds building nests, arriving and departing, and tearing with their bills as they incubate (*right*).

at least in the later stages. On the atolls of the North Pacific, there are no significant land predators, except possibly the house rat, the Polynesian rat (*Rattus exulans*), and Great Frigatebird (*Fregata minor*).

Within the primary breeding range of the Laysan Albatross, the house rat seems limited to Midway Atoll, and the Polynesian rat occurs in significant numbers, as far as I know, only on Kure Atoll. Neither preys to any extent on healthy chicks, although Kepler (1967) reported that the Polynesian rat may kill some chicks as well as incubating adults. The frigatebird breeds on several islands along with Laysans and does seize young Red-footed Boobies (*Sula sula rubripes*) from their nests several feet above ground, but we have no record of attacks on nestling albatrosses.

Once the Laysan has ceased constant brooding, it does not physically defend its chick against other albatrosses, rats, dogs, or people. But its mere presence at the nest (Figure 33) is important. In the first place, it holds a reservoir of food, available on demand, and feeds the chick several times a day for the first six days. Second, it broods the chick rather constantly for the first four to eight days; after that it may or may not shelter the chick from rain. Third, it prevents juveniles and non-breeding adults from injuring the chick by trying to brood it, and any albatross from trampling it while landing or taking off.

The attending adult shows nothing more than an awareness of the intruder. It permits other albatrosses to approach and even touch the chick, and I never saw any intruder attempt to harm a chick when the parent was alongside.

Discussion

Incubation Pouch

The pouch develops in both sexes of currently breeding birds after they arrive in the colony and before incubation begins; but it reaches its maximum size in experienced males so soon after they arrive that we believe it must begin to develop while the birds are still at sea. Older birds develop a pouch earlier than younger birds; in males earlier than in females; experienced birds, not currently breeding, may or may not have a pouch. Birds under four years of age seldom have one.

In twosomes of juveniles, both about the same age, the male's pouch is more advanced than the female's. In pairs of different ages, the older member usually develops the pouch first.

Unpaired, four- and five-year-old males, establishing territories and seeking mates, frequently have a pouch; females of the same age and phase most often do not.

From these observations, we may conclude that the development of the pouch in the Laysan Albatross is under the same hormonal control as the development of the gonads, and that the hormonal system that stimulates the bird to return to the colony also governs the development of the pouch. The fact that the enlargement of the gonads, the time of arrival in the colony, and the loss of down from the pouch are all correlated with the age of the birds (H. I. Fisher and M. L. Fisher, 1969) justifies this conclusion.

Other controlling factors — for example, a difference in the amount of stimulation by the hormonal factor — may account for the experienced birds that return but do not develop a pouch. The sexual difference in the time of development substantiates this.

Probably, the bird requires a greater stimulation — a higher hormonal level — to develop a pouch than to return to the home colony. Males that return earlier and develop the pouch sooner are exhibiting earlier or stronger responses than females to the same environmental stimuli. The fact that all females associating with males complete the pouch sooner than females not associating with males suggests that the presence of the male provides a final or summated stimulus.

The experienced breeders that returned to the colony, but did not breed, weighed considerably less than the breeding birds and showed little or no development of a pouch. This further substantiates my suggestion that Laysan Albatrosses must accumulate an energy reserve in order to breed and that a lack of such reserve prevents them from breeding (H. I. Fisher, 1967).

Length of Incubation Period

The primary period of incubation is 20 November to 18 February, but few eggs hatch after 10 February. The average length for all pairs is 65 days (55 to 72), median 64–65, as short as any reported for albatrosses. The short period in the Laysan, one of the smallest albatrosses, may be correlated in part with size.

None of the observers who recorded incubation periods for albatrosses mentioned the number of different factors that may affect the length of the period in any one pair.Tickell (1968), using nine examples, did indicate that the incubation periods of eggs laid in successive years by the same female Wandering Albatross varied as much as three days. J. Fisher (1952:366) reported variable incubation periods in the Atlantic Fulmar, from 41 to 57 days, but did not discuss the reasons.

Our study showed that the primary variables in the length of the incubation period were age and experience, the incubation period being longer in old experienced females than in young inexperienced females.

The eggs of experienced females, over seven and mostly over eight years old, were incubated an average of 65.6 days (63–72); the eggs of inexperienced females averaged 63.8 days (55–66). Since both sexes share incubation duties,

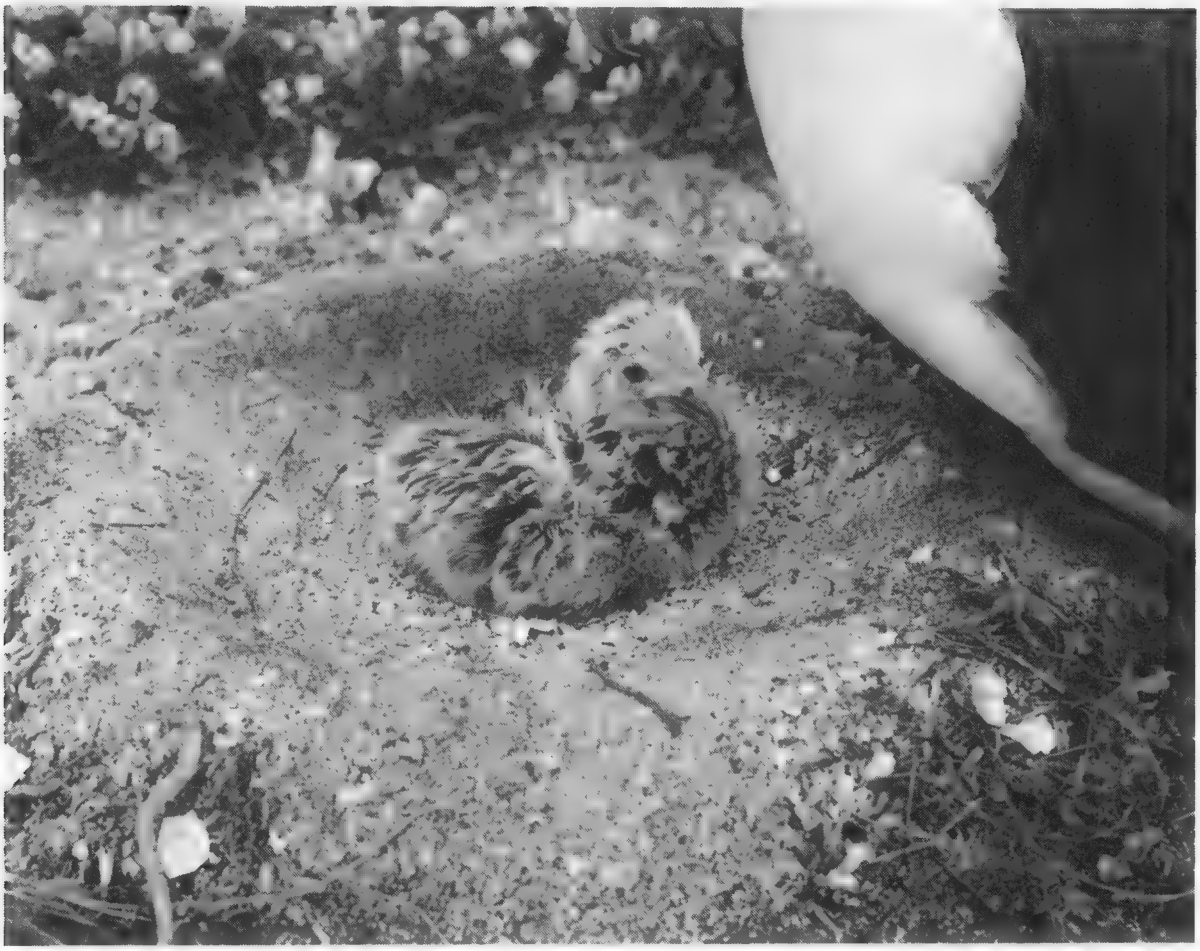


Figure 33. A ten-day-old Laysan chick is "guarded" by its parent.

the incubation periods of pairs with members of different ages might have been revealing. Unfortunately, too few of our banded birds of known age were old enough to breed when we collected our data on incubation.

Within the two age groups, the major factors that might modify incubation are the size of the egg and the amount of heat applied to it (Barott, 1937; Nice, 1954; Eklund and Charlton, 1958; Reid, 1965). The eggs of older females are larger than those of younger ones. Twenty-two eggs, laid by females in at least their tenth breeding season, averaged 112.4 mm by 68.9 mm; 12 eggs, laid by females in their first season, averaged 111.2 mm by 66.9 mm. The diameters differ enough to be statistically significant; this could mean a difference in volume great enough to affect, at least in part, the total incubation time.

We did not obtain the egg weights that might have substantiated this. However, the effect of weight on the length of the incubation period is questionable, even for our best known species, the Domestic Fowl (Byerly, 1934; Hays, 1941).

According to Howell and Bartholomew (1961a:187), the skin temperature in the incubation pouch of the Laysan varies less than one degree (mean 36.7°C) and maintains a constantly incubated egg at about 36°C. The possibility of the temperature of the pouch varying with age seems remote and they did not comment on it. Thus, it seems unlikely that individual differences in temperature are ever great enough to affect the length of the incubation periods.

The temperature of the egg drops and the development of the embryo must stop, or at least slow down, when the egg is exposed. Since an albatross egg may be left unattended for as long as five days and still hatch, one or more absences of the birds during incubation could lengthen the period. The temperature of the egg may also drop during cool rainy weather, when the ground as well as the air is cold, or when the bird just rests on the egg without fitting it into the pouch. But none of these factors would make the incubation periods of young birds shorter than those of old birds. Actually, since young birds are more prone to abandon their eggs temporarily, we should expect just the opposite — that their incubation periods would be longer instead of shorter than those of the old birds.

Because the birds that have survived longer and been more successful in reproduction have the longer incubation periods, we might speculate that the period is becoming longer through selection against the shorter period. Hatchery procedures increased the period in the Domestic Fowl by 1.5 days in 25 years (Dr. Scott Hinners, pers. commun.). Natural selection in the direction of longer incubation periods might occur because of long-time changes in the distribution of food. Ashmole and Ashmole (1967) and Lack (1968) theorized that the long incubation period in many Procellariiformes, and the ability of their eggs to withstand chilling for relatively long periods, came about through the "need" of the adults to go long distances for food. If one accepts this hypothesis, a change to more distant feeding waters might, over a long period, result in longer incubation periods. As yet we have too little information on the distribution of the food of the Procellariiformes to draw any conclusions.

Another possible explanation is that the activities of new parents, and perhaps even the unhatched chicks, affect the speed of hatching. The pipping process can take five days, but communication between the parent and the chick—as suggested by Vince (1964, 1966a, 1966b, 1968) and Gottlieb (1965, 1971) — might speed it up. Laysans may have such communication. The voices of both parents and unhatched chicks are audible to the human ear for a distance of more than three feet.

Probably some unknown behavior or the extent of some known behavior in the Laysan Albatross influences the total number of degree-days necessary for the hatching of the egg.

Whatever the cause, a great number of eggs laid late in the season hatch on the same days as those laid earlier. This simultaneous hatching may be important for the colony as a whole when, during the following summer, the fledglings going to sea from the beaches confront the sharks, their primary predator at this stage. A shorter period of departure from the nest means that the seas adjoining the beaches will be more crowded at any one time; and, the greater the numbers of fledglings, the fewer that will be victims of sharks.

Attentive Spans

In the Laysan Albatross, both members of the pair share the incubation period which usually consists of five spans starting with the female in Span 1. Thus, except during the exchange, they seldom see each other once the egg is laid, as Jameson (1961) noted in the Wandering Albatross. Tickell (1968) reported an average of 10 spans in the Wandering Albatross; Richdale (1952), nine to 16 in the Royal Albatross.

The length of any span depends on the return of the mate, which, in turn, depends on the age and experience of the mate. The first span of the female with an inexperienced mate averages twice as long as the first span of a female with an experienced mate.

In most Laysans, the last exchange occurs within ±4 days of hatching; two-thirds take place within ±2 days; and one or both parents may be present at the nest when the chick emerges.

The pattern of spans in the Laysan and Black-footed Albatrosses is evidently more regular than in other albatrosses. Studies of Laysans and Blackfoots, nearly 10 years apart, reveal constant specific features. Studies of other albatrosses took place in rather widely separated locations with much longer periods of intervening time. Because the length of the span depends upon the success of the foraging mate in finding food, differences in the location of the colony, and of the food source in different years, may cause inter-colony differences in the length of the spans in any species. I should expect, though, a considerable consistency within an age group in any one colony if the source and availability of the food remain constant.

The Laysan male does the greater share of incubating and averages 36 days against 29 days for the female; we recorded only two instances of females incubating longer than males. Rice and Kenyon (1962b:542) found that the Laysan male incubated 53 per cent of the period. This is characteristic of albatrosses. Tickell (1968:25) stated that the male Wandering Albatross averages 41.8 days and the female, 38.5 days, and added that male Wandering and Royal Albatrosses "... habitually assume the greater proportion in some pairs but the female is dominant in others. In still other pairs either bird may take the larger share of the incubating." Richdale (1952) wrote that the male Royal Albatross spent 41.3 days and the female 40.5 and suggested, but did not verify, that the male Buller's Mollymawk spent more time on the egg than the female. Rice and Kenyon (1962b) reported the same situation for the Black-footed Albatross.

The male's total time is longer mainly because the first span of the female is very short. We believe that the male, in good physical condition at this time, does not go far from shore during Span 1 and is able to return quickly, a behavioral adaptation equalizing the total energy drain on male and female during incubation. Tickell (1968) thought that the first span of the female Wandering Albatross was short mainly because of the male's dominance and ability to "take over." Richdale (1949a, b) felt the same about Buller's Mollymawk and the Royal Albatross, but later (1950) intimated that the renewed energy resources of the male were also responsible.

A study of body weights of Laysans throughout the season showed that the energy expended by both sexes may be nearly equal throughout the breeding season (H. I. Fisher, 1967). If the energy drain is equal, the heavier male can incubate longer before his weight drops to the dangerously low level that results in desertion.

When the female begins her first span, her weight is down. The energy expended in the production of an egg, equal to approximately 10 per cent of her weight, perhaps approaches the energy used in a week or more of incubation. The male, on the other hand, begins his first span (Span 2) at nearly maximum weight. The few observers who have contended that the male begins incubation probably failed to note the females that incubated only a few hours.

Most students of albatrosses have reported that the spans grow progressively shorter as hatching time approaches. One might hypothesize that the energy requirements are so much greater than the energy intake during incubation that the birds must return to the sea for food with increasing frequency. However, this does not seem to be the case. Our study of body weights showed that an incubating Laysan, released from its duties, regains the weight lost, approximately 20 per cent, during the next long span (20 ± days) of its mate (H. I. Fisher, 1967), and that the "basic survival weight," judged by the weights of birds that deserted after abnormally long spans, is some 1600 to 1900 gms. The weights of birds whose spans terminate with the return of the mate usually exceed this basic weight by 500 gms, a significant safety factor for bird and egg.

Regular, seasonal differences in the distribution and abundance of food may account for the shorter spans, but we have no evidence. We do know that the shortening spans lead to a pattern whereby each parent, after the guard phase, feeds the chick every other day.

The shorter spans also mean that the parent on duty at hatching will have food and oil for the chick. The digestive tracts of Laysan Albatrosses, which have incubated as long as a week, contain neither food nor oil. The oil, known to be a secretion of the proventriculus, and not entirely dependent on the presence of food in the digestive tract, first appears in the stomach of the incubating bird seven to 10 days before the chick hatches. However, oil alone does not sustain the chick in the first few days. When the energy reserves in the yolk sac are exhausted, the chick must have food — a mixture of partly digested squids and fishes — and oil perhaps in part derived directly from the food. Therefore, recent feeding by the adult may be as vitally important to the albatross chick, as it is to the chicks of the Atlantic Fulmar (J. Fisher, 1952: 368–369) and the Adelie Penguin, *Pygoscelis adeliae* (Reid, 1965; Reid and Bailey, 1966).

Supporting this hypothesis is the fact that the first span of the guard phase, when the same adult broods the chick constantly and feeds it repeatedly, averages no more than two or three days (Rice and Kenyon, 1962b:550).

The pattern of exchanges nearest the hatching time are very likely important to the survival of the chick, not the embryo, and the sex of the parent present at hatching is unimportant. This may be usual in far-ranging birds with long incubation periods, as suggested, for example, in the Royal Albatross (Sorenson, 1950a) and in Fulmars (Carrick and Dunnet, 1954).

The pattern of spans varies from pair to pair, despite the overall similarity within the species. When major variations occur in the first and second spans, the birds often adjust the length of later spans so that the total time spent by each sex is close to average.

Since the length of a normal span depends upon the return of the mate, any bird forced to incubate for an unduly long span may require a longer time to feed, and this, in turn, may lengthen its mate's span. A series of shorter-than-usual spans could also result when the early spans are shorter and require less energy. The relieved birds, more quickly satisfied, might return sooner than expected. Good weather and a supply of food nearby could mean more shorter-than-average spans. Though we rather expected a yearly variation, we did not find it.

Any species, whose incubation period exceeds in length and stress the capabilities of one parent, must have complex and specific patterns for sharing the duties. When the period is long and the food source generally distant, the problem increases. Within the order Procellariiformes, the "solution" is a nearly equal sharing of nesting duties, prolonged incubation spans that permit the off-duty member to forage far, and a species-specific pattern of spans and time. Various studies indicate this: Laysan Albatross (Rice and Kenyon, 1962b, and this study), Black-footed Albatross (Rice and Kenyon, 1962b), Royal Albatross (Sorenson, 1950a; Richdale, 1952; Tickell, 1968), Buller's Mollymawk (Richdale, 1949b, 1952), Wandering Albatross (Jameson, 1961; Tickell, 1968), Dove Prion, *Pachyptila desolata* (Tickell, 1962), and Short-tailed Shearwater, *Puffinus tenuirostris* (Marshall and Serventy, 1956).

Apparent also from these studies is the fact that the length of the individual attentive periods varies interspecifically with body size. The spans are longest in some albatrosses, intermediate in the larger shearwaters, and shortest in the small petrels.

Hatching Success

On Midway, 92 per cent of the chicks hatch between 28 January and 5 February; nearly 50 per cent hatch before 1 February. These dates may be different by a week or more in Laysan colonies to the southeast in the Leeward Islands of Hawaii. The breeding dates of the Royal Albatross differ by three weeks between northern and southern New Zealand (Sorenson, 1950a).

The hatching success, normally about 70 per cent, dropped to 56 per cent in 1964-1965 and the breeding population was only half those of the preceding and following seasons. An increase in desertions and infertile eggs accounted for the low success, but the causes of both increases are obscure. An unusual number of desertions occurred during the several spells of extremely bad weather, but similar weather in other seasons did not cause a comparable number of desertions. Since so many former breeders were present but not breeding, since the weight of most birds was lower than normal, and since infertility was high among those that tried to breed, probably something more than local storms caused the low success. Very likely even the breeding birds had less energy reserve and greater energy stress than usual and thus were more prone to abandon the eggs.

Hadden (1941:33) reported "... only about a 5 per cent failure. ..." in nesting, but we do not know whether he referred to the total eggs laid or the eggs remaining at hatching time. Rice and Kenyon (1962a:372) reported nest mortality as "... 6 per cent per month. ..." but in their major paper on the breeding of the Laysan Albatross (1962b) I find no direct mention of the rates of nest loss. However, their data (Table 2, page 521) suggest a loss of 56 per cent in the 1956–1957 season. Westerskov (1963:802) stated that Royal Albatrosses on Campbell Island hatched nearly 90 per cent of 101 eggs, but earlier (1958, 1960) he referred to a 75 per cent hatching success. Tickell (1968:43) recorded a 72 per cent hatching success in the Wandering Albatross. Carrick and Dunnet (1954) stated that nest losses in the Fulmar ranged from 18 to over 50 per cent, with the greatest losses in the largest colonies.

More eggs of experienced than of inexperienced females hatch — 66 to 82 per cent versus about 50 per cent — but more than experience seems to be involved. The time of laying appears to be important. Experienced females lay earlier in the season than inexperienced females. And in the young females, 54 per cent of the eggs laid early hatch while only 44 per cent of those laid late hatch; less than one-third of all eggs laid the last week of the season are successful. A similar progressive decrease in success apparently occurs in the Kittiwake, *Rissa tridactyla* (Coulson and White, 1958), and the Manx Shearwater, *Procellaria puffinus* (Matthews, 1954). I have no explanation.

The net result is that young females contribute very few chicks at hatching time and lose a greater portion in the later stages (H. I. Fisher, MS).

Loss of Nests and Eggs

On Midway, the three major and regular causes of nest failure are: abandonment, infertility, and human disturbance. Less significant and more variable are storms. Miscellaneous causes include rats, chilling of the egg, loss of mate, displacement of egg, puncture of egg, and interference by other albatrosses. In considering the importance of these we must remember that the Laysan Albatross has never been known to renest.

Desertions cause an average of 20 to 30 per cent of all losses and occur at a fairly even rate throughout incubation, lessening slightly near hatching time perhaps because of the additional stimulus provided by *peeps* from the chick in the egg and by the more frequent presence of the mate.

There is no sexual difference in desertions. Some individuals are more prone to desert than others, abandoning their eggs year after year.

Birds desert more frequently in the first two breeding seasons than later. Possibly the ability to produce an egg develops at an earlier age than the ability to incubate for long periods; perhaps the young birds lay prematurely and gain experience that will be useful in future years when their success is more vital to the species.

Because two-thirds of all desertions occur during the long spans — Span 2 by the male and Span 3 by the female — one might suspect that the cause was related to the failure of the mate to return on schedule. Surprisingly, however, most birds desert in the early days of these spans. Only 18 per cent desert when the spans are longer than average.

Unusually severe storms may produce, in a few days, two-fifths of all the desertions that season.

Desertion has no effect on a bird's return to breed the following season: 76 per cent of the deserters return, a rate that compares well with the 70 to 80 per cent return of adults that reared chicks. Rice and Kenyon (1962b:521) reported that 12 per cent more of the breeders that lost eggs early in the season returned than those that lost eggs late in the season. I suspect that any discrepancy between our data and those of Rice and Kenyon is related to the food available in different years. Other information leads me to believe that one season of their study, 1956–1957, was poor for albatrosses breeding on Midway.

Infertility ranges from a low of three to five per cent to a high of 16 per cent. Rice and Kenyon (1962b) found 75 (18 per cent) of 419 eggs infertile. Tickell (1968:44) reported 7.2 per cent for the Wandering Albatross, and Richdale (1952), 2.6 per cent for the Royal Albatross. Our high rates for the Laysans, and perhaps those of Rice and Kenyon, correlate with low numbers of breeding adults and a low nest success. Thus, infertility may be partly related to low energy reserves or an absence of a particular nutrient in the diet. Until we know more about the diets of breeding albatrosses, we can only speculate.

Today human beings constitute a disturbance, either direct or indirect, only on Niihau Island, French Frigate Shoals, and Kure and Midway Atolls. The well-documented depredations on Laysan Island no longer occur, and disturbance is negligible on French Frigate and Kure. On Niihau Island, where feral swine once eliminated much of the breeding colony (H. I. Fisher, 1951), Mr. A. F. Robinson (Rice and Kenyon, 1962a:377–378) stated that the birds were now more numerous than before World War II. On Midway, human disturbance perhaps accounts for an average loss of less than three per cent.

With the US Navy's variable enforcement of strict regulations, eggs and nesting birds or their mates are sometimes destroyed. The control program, which started in 1956–1957, eliminated nearly one-fourth of the nesting area and resulted in the deaths of thousands of breeding birds (H. I. Fisher, 1966); it is largely dormant now. As far as I can determine, the last nest destruction over a wide area was in 1965; the killing and destruction of nests along the runways continues, but it is sporadic and limited in scope.

The direct effect of storms is great in situations where water from heavy rainfalls accumulates or waves reach the colonies. The nests of Black-footed Albatrosses on exposed shores nearer the ocean suffer more from wind and waves than the Laysan nests. The literature shows that such loss is widespread on the low-lying islands that form the limited breeding grounds of the Laysan. Willett (1936) described a loss in 1913 of "3,000" albatross nests by the rising water in the lagoon of Laysan Island. On 9 March 1957, a tidal wave washed away and drowned many chicks of both species on Midway (Rice, 1959:19–20). Rice also noted that a 30-foot surf, 11–13 January 1958, destroyed about 42 per cent of the nests of Black-footed Albatrosses and some of the Laysans. On the low islets at Pearl and Hermes Reef, the same storm wiped out perhaps 50 per cent of the Laysan nests. And finally, Richardson (1954) described a mid-January storm that destroyed all but two albatross eggs on Tern Island of French Frigate Shoals.

The chilling of an egg is the result of temporary or successive abandonment by one or both parents. Although the relatives of the Laysan Albatross in the Southern Hemisphere nest in much lower temperatures, midwinter on Midway is not always as equitable and mild as Howell and Bartholomew (1961a, b) described. Eggs chill rapidly when temperatures in the low 50's combine with high winds. Despite this, chilling of eggs, especially in the first two weeks of incubation, causes few nest failures. Laysan eggs, exposed several days or for a day or so on several occasions, still hatch, as Hadden (1941) also noted. The eggs of Manx Shearwaters, chilled from seven to 13 days, hatched (Matthews, 1954), and eggs of the Dove Prion, exposed up to six days, hatched (Tickell, 1962). Other procellariiforms show similar potentials.

The ability of the egg to withstand chilling is of great value to species that have long incubation periods in adverse climates, complex patterns for sharing nesting duties, and long flights for food.

One of the most common, and unexplained, relationships during the incubation period is the presence of hundreds of ants on the abdomen and breast of incubating birds. We found them on most birds every year. The heavy mucous on the eggshell, the bloody exudates from the female's cloaca, and the procellariiform odor apparently attract them, and they move quickly from the coral soil to the bird on the nest.

The ants swarm on adults newly arrived from the sea and die in a day or so, but not from crushing. The contact with the feathers or the ingestion of something on the feathers apparently kills them. Adult birds pay no attention to the ants; very young chicks scratch and shake their heads. Living ants often cover weak and dying chicks. Since ants are alive on chicks and dead on the adults, it is possible the oil film or the salt water kills them.

Insects sometimes cause birds to desert their nests. R. T. Peterson (pers. commun.) told me that occasional and severe infestations of mosquitoes sometimes force the Galapagos Albatross to abandon its nest. But we found no evidence that ants ever cause egg loss directly or indirectly in the Laysan Albatross.

Summary

This report is based on data collected during the breeding seasons from 1961 to 1969 at Midway Atoll in the North Pacific where my associates and I have marked 99 per cent of the Laysan Albatrosses (*Diomedea immutabilis*) and their nests in a permanent research plot. We have information on approximately 5,300 nesting pairs and detailed data on 1,446 nests in the three seasons. We checked every nest, bird, and egg or chick each morning during incubation. By 1969, we knew the age, within a month, of many birds in the plot.

Before incubation begins, all currently breeding birds lose the down from a portion of the abdominal apterium and develop an incubation pouch that averages 50 by 95 mm and accommodates only one egg. The time of development varies with sex and age — males before females, experienced birds before inexperienced birds. Non-breeders may or may not have a pouch; birds under four years of age never have one. In most birds, refeathering begins in February and is complete by 1 March.

The incubation period for all birds averaged 65 days; a sample of eggs of experienced females, laid early in the season, averaged 65.6 days; eggs of inexperienced birds, laid later, averaged 63.8 days. In one season, eggs deposited before 3 December averaged 65.4 days; eggs laid after 2 December, 64.7 days; the first 50 eggs in the colony, 65.4 days; and the last 50 eggs averaged 64.3 days. The incubation period for the colony extends from 20 November to 18 February; 97 per cent of the birds begin incubation before 7 December.

Both members of the pair share the incubation duties in a series of spans — a span being a continuous setting by one bird. The female takes Span 1. The usual number of spans is five; Spans 6 and 7 are rare. Ninety-five per cent of the eggs hatch before Span 6; of these, 75 per cent hatch in Span 5 and 20 per cent in Span 4. Span 1 is short — modal time under 24 hours — and is shorter for experienced birds than for inexperienced birds. Span 2 is usually the longest, and succeeding spans grow progressively shorter until hatching. The male averages more time on the egg than the female — 36 ± 1 versus 29 ± 1 days. When one member has an extra long span, the lengths of the other spans are usually adjusted.

The hatching period is from 23–25 January to 14–19 February with the main peak from 28 January to 5 February, when the eggs of the experienced pairs hatch. A smaller peak occurs from 7 to 18 February when the eggs of the inexperienced pairs and experienced birds with new mates hatch. The egg may pip six days before hatching, but pipping time averages from two to four days. Adults never aid the hatching or remove the egg shells.

The colonywide hatching success averages 70 per cent. Eggs laid early in the season or by more experienced females are less subject to loss than those laid later or by inexperienced females.

Although desertions are the chief cause of nest loss on Midway, many other factors play a part. In some years storms are very destructive. Rats take abandoned or temporarily abandoned eggs and weak chicks; eggs roll out of nests; fumes from a fuel farm may kill birds on their nests; men slaughter some birds and take over the nesting areas of others; birds crack their own eggs; non-breeders take over eggs; and some eggs are infertile. Desertions occur fairly regularly throughout the season, many in Spans 2 and 3 and in the beginning of all spans. The causes of desertions and estimates of the effect of each of the other factors on the success of the nests are listed.

Copulation establishes the chronology for the succeeding events in the entire reproductive season.

The urge to copulate is strong in males which reach their stations first and wait for the females. We distinguish here between true copulation by members of the pairs on the male's station and "rape attempts" which involve groups of birds.

The age of the pair-bond and, to a certain extent, the age of the birds determine the number and type of precopulatory signals. Experienced pairs may copulate within an hour after the female returns; young birds may wait longer, even overnight, and employ more precopulatory signals. The male's bill over the back or neck of the female in submissive posture, spread wings and bent head, is an immediate precursor of copulation. True copulation is relatively subdued, never interrupted by adjacent males, lasts two or three minutes, and is rarely repeated. After copulation, the birds circle the site, bill-touch, mutual-preen, and utter *eh ehs*. Within two to five hours they usually depart for the sea where they spend eight days, more or less. The male Laysan very rarely copulates with any female other than his mate and almost never with an incubating female. Non-breeders may copulate occasionally, but only with the mate; birds less than six years old seldom copulate. Rape attempts, when a group of males tries to copulate with a female or a male in a submissive position, are never successful. In examining hundreds of birds involved in rape attempts, we never found evidence of cloacal contact, either mucous exudate or sperm. The female Laysan Albatross, by her refusal to copulate with males other than her mate, preserves monogamy in this species.

The rather rigid schedule of events that follow copulation is outlined and described: nest initiation by the female; nest completion by the male; activities of the incubating bird; defense of nest and nest-site tenacity; the spacing of nests; behavior during storms; recognition of mates; exchanges at the nest; interference by other albatrosses; desertion and the return of the deserters to the colony; looking at the egg; talking to the egg; alarm notes; nonsense behavior; and the guard phase.

The hormonal system that governs the development of the gonads and the return of the bird to the colony also controls the development of the pouch. The correlation of these three events with the age and sex of the albatross indicates this. Why some birds return and do not breed is a question. Possibly, albatrosses need more stimulation to develop the pouch and to breed than to return to the colony. The fact that the body weights of non-breeders average less than those of breeding birds suggests that albatrosses may also require an energy reserve at the beginning of the breeding period.

The average length of the incubation period in the Laysan is as short (65 days) as any reported for albatrosses and may be correlated with body size — the Laysan is one of the smallest albatrosses.

Age and experience are the major variables affecting the length of the incubation period. The eggs of old experienced females are usually larger and take longer to hatch than those of young inexperienced females. Eggs laid late in the season are incubated for a shorter time than those laid early. It appears that natural selection is working toward the longer period.

Whatever the cause, many eggs hatch in a short period, and the following summer many young simultaneously leave the beaches for the sea. Since there is "safety in numbers," fewer become the victims of sharks than if they left in small groups.

The pattern of incubation spans appears to be more precise and regular in the Laysan Albatross than in Southern Hemisphere albatrosses. The length of the individual span depends upon the return of the mate, which, in turn, partly depends on its success in finding food. The female Laysan, in producing an egg that is 10 per cent of her weight, may expend about as much energy as she would use in incubating that egg for one week. The male offsets her loss by taking over the major share of the incubation. Both birds normally regain all weight lost in one long span during the following interval at sea and stay well above the minimal weight that results in desertion. Thus, the spans do not shorten before hatching time because the adults need food. The spans probably grow shorter because one adult, newly arrived from the sea with a supply of food and oil in its gullet, must be on hand to feed the newly hatched chick. The shortening spans also prepare for the time, following the guard stage, when each parent feeds the chick every other day.

The hatching success was constant over the years, about 70 per cent. The 1964–1965 season was an exception — only 56 per cent success; the colony was smaller, the proportion of desertions and infertile eggs greater, and the average weight of all birds lower. I suspect that some factor outside the local area prevented many of the birds from building up the energy reserve necessary for breeding that season.

Our data showed that the three major causes of nest loss on Midway were desertions, 20 to 30 per cent; infertility, usually three to five per cent but sometimes as high as 16 per cent; and human disturbance, less than three per cent.

Except during severe storms, the rate of desertions is fairly steady, lessening just before hatching. It is about equal between the sexes and higher in young birds than in old. Most desertions occur in the long spans, and at the beginning of all spans when we are certain that hunger is not their cause. Some albatrosses are chronic deserters, year after year; many others nest successfully the season following a desertion. It may be that inexperienced birds, which desert more often and have a greater proportion of nest failures, are in a "practice period" preparing for the time when their nests will be more important to the survival of the colony.

Infertility may be related to low energy reserves caused by a lack of food or a change in the food source. We know too little about the food and feeding habits of Laysans to speculate further at this time.

The disturbance caused by human activity on Midway is at present much reduced. The strict regulations of the Navy, though variably enforced, have helped lower the loss of birds, nests, and eggs.

Storms are the most variable of the destructive forces, causing from zero to five per cent of the losses.

Other more regular losses, direct and indirect, result from rats, chilling of the egg, death of a mate, displacement of the egg, breakage of the egg, and interference by other Laysans. Insects seem to be no problem. Although ants swarm over adults newly arrived from the sea and some of the chicks, we have no evidence that they ever cause death of a chick or desertion by an adult.

Acknowledgments

This paper presents the results of one part of a long-range investigation of the biology of the Laysan Albatross for which the Office of Naval Research (contract ONR 3479 (00) 107-599) and Southern Illinois University provided financial aid. The University has also been most generous in allowing me time from campus commitments to visit Midway during the incubation seasons of these nine years.

Without the logistic support provided by the naval commands on Midway during these years, the research would have been much more arduous and much less pleasant and successful. I cannot mention all navy personnel who helped, but I make special note of aid "beyond the call of duty" from Captain George Washington Davis V, Captain Fred Milner, Captain A. S. Yesensky, and Captain J. Anderson.

My wife, Mildred, maintained records, prepared summaries from them, always lent a sympathetic ear to incessant talk about "my albatross," and, best of all, loyally supported my determination to learn everything possible about this species.

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ON THE BIOLOGY OF THE AMERICAN FINFOOT IN SOUTHERN MEXICO

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Photographs by the author

Along the tropical streams and rivers on three continents dwell relatively uncommon birds called sun-grebes or finfoots — three species, one on each continent. Comprising a distinct family (Heliornithidae), these three species appear to be most closely related, on morphological grounds, to rails. Superficially similar to rails, the finfoots have grebe-like bills, lobed toes, and short legs placed far back on the body. Extremely secretive and inconspicuously marked, they live along the margins of tropical streams and rivers, seeking a variety of food, including insects, crustaceans, frogs, and molluscs. The females are usually slightly smaller and bear somewhat more vivid markings than the males; unlike the grebes, both sexes have a well-developed tail.

The bills and feet are different in all three species. The large African Finfoot (*Podica senegalensis*) is over two feet long, has bright red feet and bill, and ranges from south of the Sahara to South Africa. The Asian Finfoot (*Heliopais personata*), the medium-sized, has green legs and a yellow bill and inhabits Sumatra, Malaysia, Thailand, Burma, and eastern India. The American Finfoot (*Heliornis fulica*), the smallest, has conspicuously banded black and yellow feet and a red bill. It ranges from southern Mexico to northeastern Argentina and is the subject of this paper. For simplicity I shall refer to this bird as the finfoot or *Heliornis*.

The literature contains almost nothing of the natural history of the American Finfoot. By making periodic observations of this secretive bird for several years, I finally discovered its nest in April 1969 (Alvarez del Toro, 1970).

Habitat

In southern Mexico, the finfoot lives along arroyos and slowly flowing rivers with wooded margins and on the edges of lakes, in the lowlands, apparently no more than 100 meters above sea level. Generally considered rare, it is relatively common in remote places in Chiapas — around Jaurez, the Lacandona region, and the fresh water swamps of the coastal estuaries (Figure 1).

The American Finfoot prefers dwelling in still water — in deep, slow-moving streams, quiet bends of bigger rivers, and along the edges of ponds.

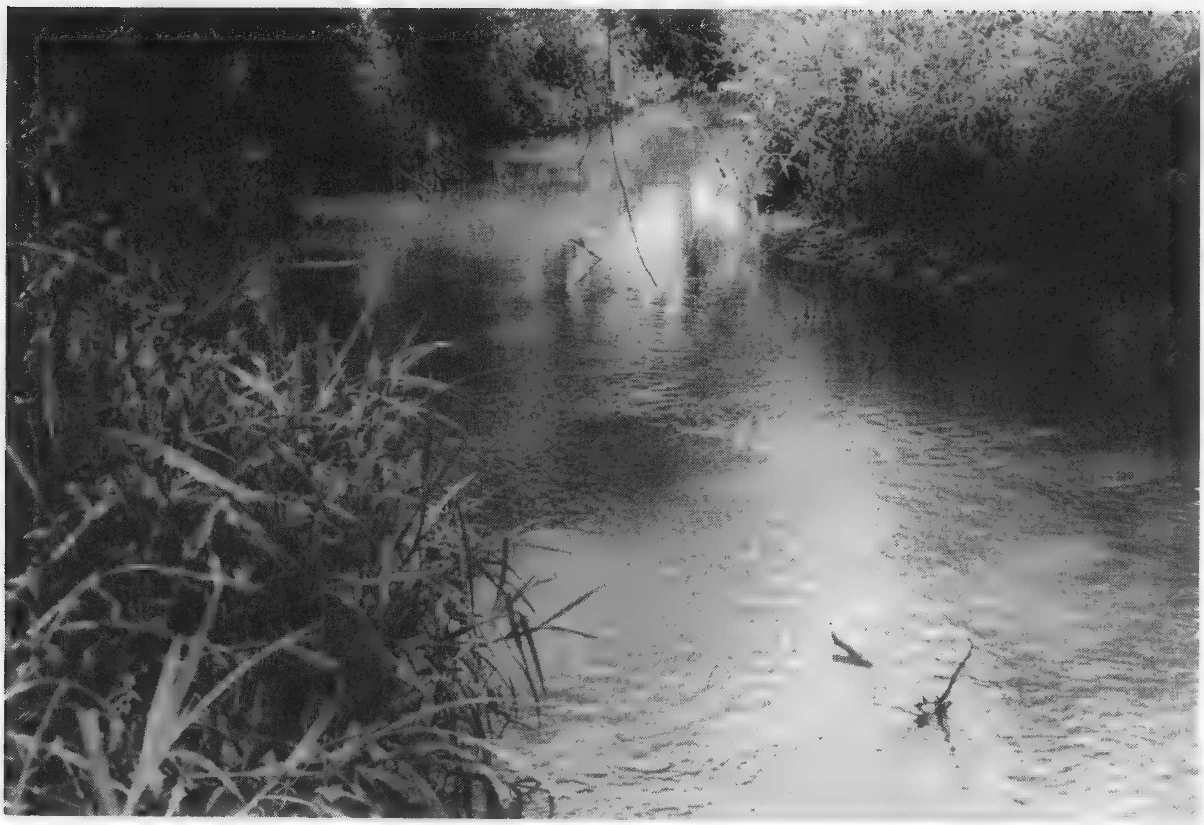


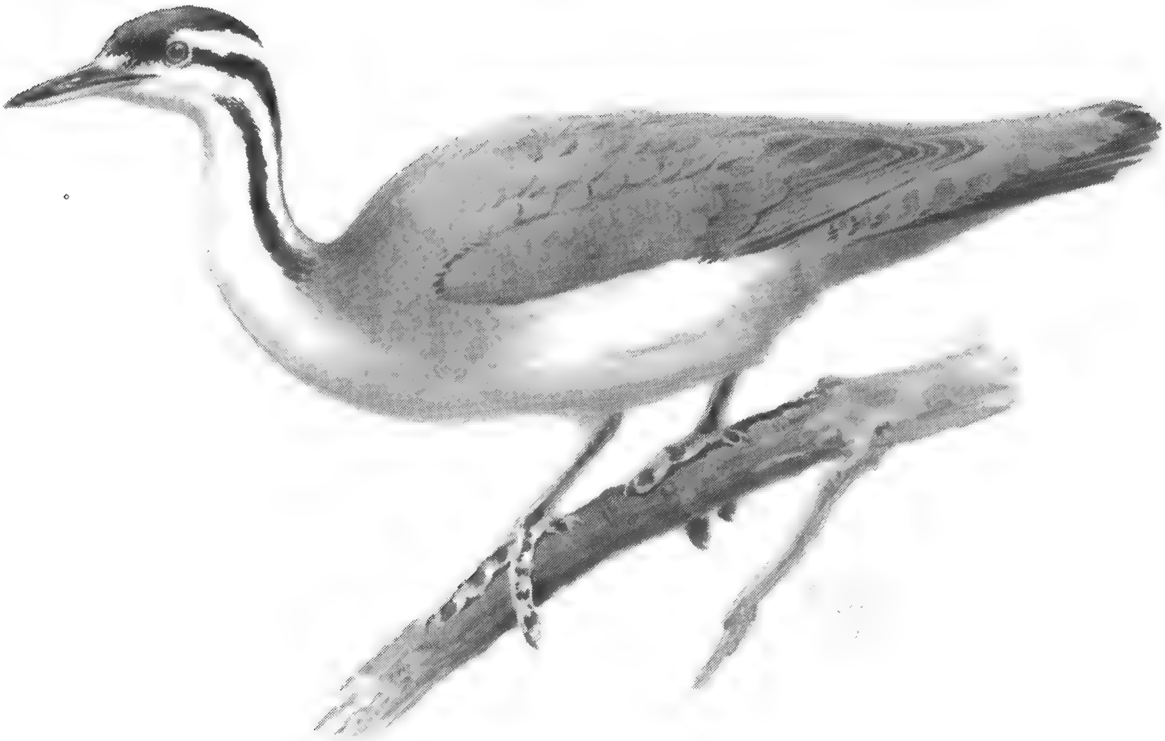
Figure 1. A small stream in southern Chiapas, Mexico, showing the typical habitat of the American Finfoot and the site of this study.

General Activity

The finfoot becomes active at daybreak, moving along the bank and feeding. Its diet, chiefly of aquatic insects and their larvae, may also include small fish, tadpoles, and some wild seeds. Sometimes, it catches dragonflies. From about 09:00 until 16:00 hours, the finfoot spends much of its time resting, either floating in a shaded watery glade or, more frequently, perched less than a meter above the surface of the water. When perched, the bird preens and, occasionally, drops to the water to capture an insect floating by. From 16:00 until dusk, it resumes active feeding on the water. At dark, it climbs with pronounced difficulty, fluttering its wings, into the lianas or branches that hang low over the stream. Very rarely does it fly to a perch.

The finfoot sleeps, hidden in dense vegetation, never on an exposed branch. If something frightens it during the night, it drops, without hesitation, into the water. At such times, crocodiles and caimans constitute a real danger. Using a flashlight, I searched for finfoots at night, and because I flushed one from the same perch on several occasions, I suspect that an individual bird roosts in the same site night after night.

These secretive birds always swim near the bank and very rarely venture into the middle of the stream except when passing from one bank to another. When escaping from danger, real or potential, the finfoot almost always swims. Very occasionally, one flies just above the water for a short stretch, and just once I saw one dive. This bird came up under floating debris and overhanging vegetation and floated with little more than its bill above the surface of the water. The heavy growth of plants along the water's edge affords a protective cover into which the finfoots often climb to hide.



American Finfoot, *Heliornis fulica.*

Illustration by George Miksch Sutton.

Territoriality

The male finfoot maintains a territory, which includes about 200 meters along the bank of a stream, and appears to remain on it the year round. Once in a while, territorial birds advertise their property right with a call. If a bird on his territory sights a trespassing finfoot, he calls several times and hurriedly approaches the intruder, which generally flees, stopping only when he reaches the boundary of his own territory. Then, each rival male performs an elaborate agonistic display, usually swimming in circles counter to the direction of the opponent's circles so that the two males come face to face at each turn. While swimming in these circles, each bird extends his neck forward parallel to the water, half raises his wings, and skims the water with his bill. The two birds circumscribe smaller and smaller circles until finally their bodies nearly touch. At this point, they fight, striking each other with their bills, jumping from the water, and flapping their wings until one bird breaks off and flees.

The encounter may last five or six minutes. Sometimes, only the territorial male circles for a time and then moves away; and sometimes, the agonistic circling may occur within the territory of one of the males instead of on their common boundary. The intruder, chased by his rival to the boundary, invariably flees. The victor swims back into his own area, frequently uttering a characteristic call, which the defeated male answers from a safe distance.

Since the two sexes appear identical for most of the year, I could not determine whether the male alone defends the territory. Nor could I determine this even after the birds had recently paired, when the female still wore the duller plumage so like that of the male. Later, during nest-building and incubation, both sexes are antagonistic toward other finfoots.

When swimming along the bank, the male, from time to time, emits a call — a short, sonorous "laugh" — that I can best describe phonetically as *eeyooo, eeyooo, eeyoo-eeyaaa, eeyaaa,* rather similar to the calls of some grebes.

Courtship

For most of the year the finfoots are solitary birds, living all alone; but, in late February, when the male emits his advertisement call more frequently and a female joins him, they swim along the territorial boundaries together. After pair-formation the male calls less frequently.

Their courtship display resembles the antagonistic display between males in that the male and female swim in counter circles with necks fully outstretched and held parallel to the water, and with wings partially raised in swan-like fashion. Both birds give a soft *cluck* sound. Describing ever smaller circles, the swimming birds eventually touch one another, at which point the male mounts and copulates. Postcopulatory display involves wing-flapping and body-shaking. The pair then swims off together.

About mid-March, the bill of the female changes from dull red to scarlet; the eyelids turn red; and the cheeks and the sides of the neck acquire a patch of golden brown feathers. The golden brown feathers are molted when the nesting season is over.

Nesting

On 15 April 1969, on the lands of the Rancho Alejandria, Municipio de Jaurez, Chiapas, I discovered a nearly completed nest of a finfoot — a thick platform, almost flat but with a slight hollow just deep enough to keep the

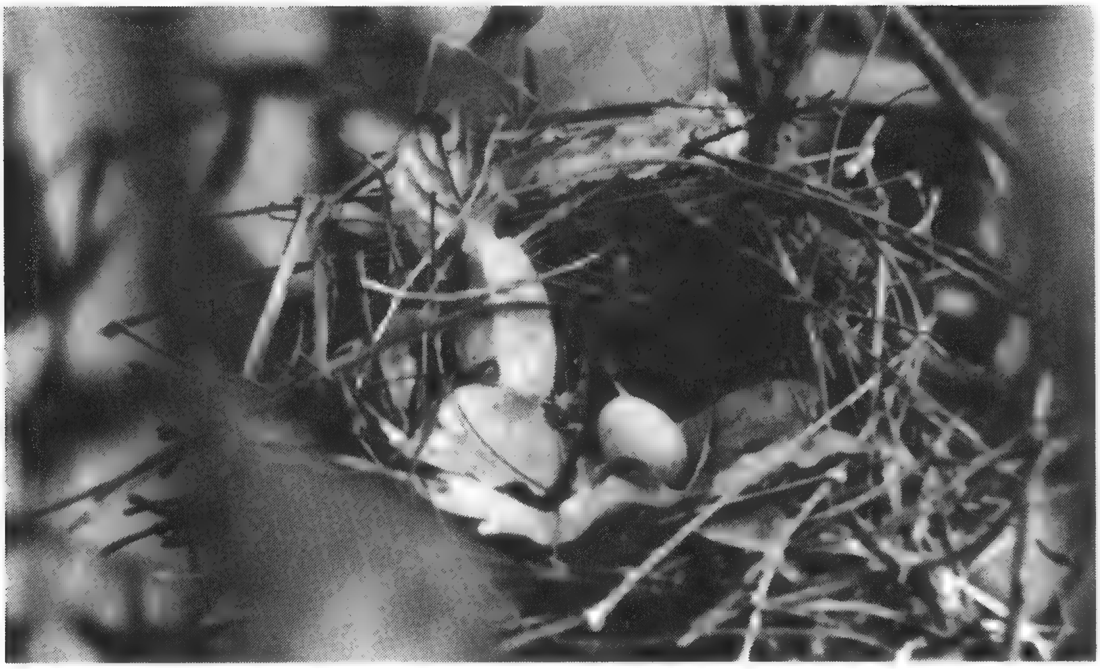


Figure 2. A pair of finfoots construct a platform of twigs in a tangle of vegetation overhanging the water. This shallow cup contains a single egg; there will be a second.

eggs from rolling out. The nest platform, about 90 centimeters above the surface of the river, rested on lianas and branches that lay directly on the water. The nest was made of sticks and lined with dead leaves. The platform, 22 cm across and seven cm deep, looked bulky and unstable, but held up well against the wind and the movements of the birds (Figure 2). I constructed an observation blind some five meters away.

The nest contained one egg when I discovered it. The following day, the female was on it when I checked at 07:00. Two hours later, she departed and there were two eggs in the nest. They were oblong in shape, pale cinnamon in color with a sprinkling of numerous, irregular, reddish-brown spots; and measured 30 x 20 millimeters and 29 x 20 mm. Soon after the female left, the male appeared, holding a leaf in his bill. He climbed into the nest, added the leaf to the lining, and then sat on the eggs (Figure 3).

The two sexes cooperated in nest construction and incubation. From the beginning of incubation, the female came to the nest at about 16:00 every day and stayed on the eggs all night and during the early morning hours. When the male appeared about 09:00, the female left to feed and did not return to resume incubation until the late afternoon. The hours of attentiveness changed gradually during the incubation period until, at eight days, the female stayed on the nest until 10:00 and did not return until dusk at 18:30.

Each bird, while on the nest, spent some time rearranging the leaves and sticks in the nest, rotated the eggs periodically, and changed position. The male, during his attentive period, often dropped down to the water to capture an insect or grab a floating leaf, and then climbed back into the nest and added the leaf to the lining. He also left the nest for short periods, swimming about in the immediate vicinity or perching on a branch overhanging the water and preening. When one bird was attentive, the other periodically visited the nest and usually added a leaf or a twig to the lining. During these visits, both birds often uttered a low *cluck*. Occasionally, they came to the nest with a short flight over the water; then they climbed slowly up the lianas that hung into the water. When leaving the nest, they simply dropped into the river like balls of cotton without producing a splash or noise.

If another bird approached the nest while the finfoot was taking a short rest period, he returned immediately. If the other bird came too close, the finfoot chased it a short distance. While I watched the nest, I saw various species of birds in the area. The finfoot's response varied not only with the proximity of the intruder, but also with the particular species. It returned leisurely to the nest when the Squirrel Cuckoo (*Piaya cayana*), Striped Cuckoo (*Tapera naevia*), Groove-billed Ani (*Crotophaga sulcirostris*), Golden-fronted Woodpecker (*Centurus aurifrons*), and Clay-colored Robin (*Turdus grayi*) appeared nearby. A pair of Green Herons (*Butorides virescens*) that nested about six meters away and often perched only one meter from the incubating finfoots never seemed to alarm them. On the other hand, if White-tipped Brown Jays (*Psilorhinus mexicanus*) or Melodious Blackbirds (*Dives dives*) appeared in nearby trees or approached the nest, the finfoot was restless. If the finfoot was off the nest, it hastily returned and threatened the intruders with plumage erect and bill open.

Hatching

On the afternoon of 26 April, the male incubated as usual. Seeing me, he showed a definite reluctance to leave the nest and, furthermore, kept his bill open as if threatening. As I approached the nest, he dropped into the river and swam to the opposite bank where he hid in the thicket that hung over the water. This behavior was quite unlike any I had encountered earlier when he, upon leaving, had moved either up or downstream and disappeared around a bend.

Puzzled by the male's behavior, I glanced at the nest and found, to my dismay, only empty eggshells. I picked up a shell and was surprised to note that it showed all the signs of normal hatching; but I could not find the chicks.

Figure 3. The male on the nest. Both sexes incubate, the male during most of the day, the female from late afternoon until the following morning.

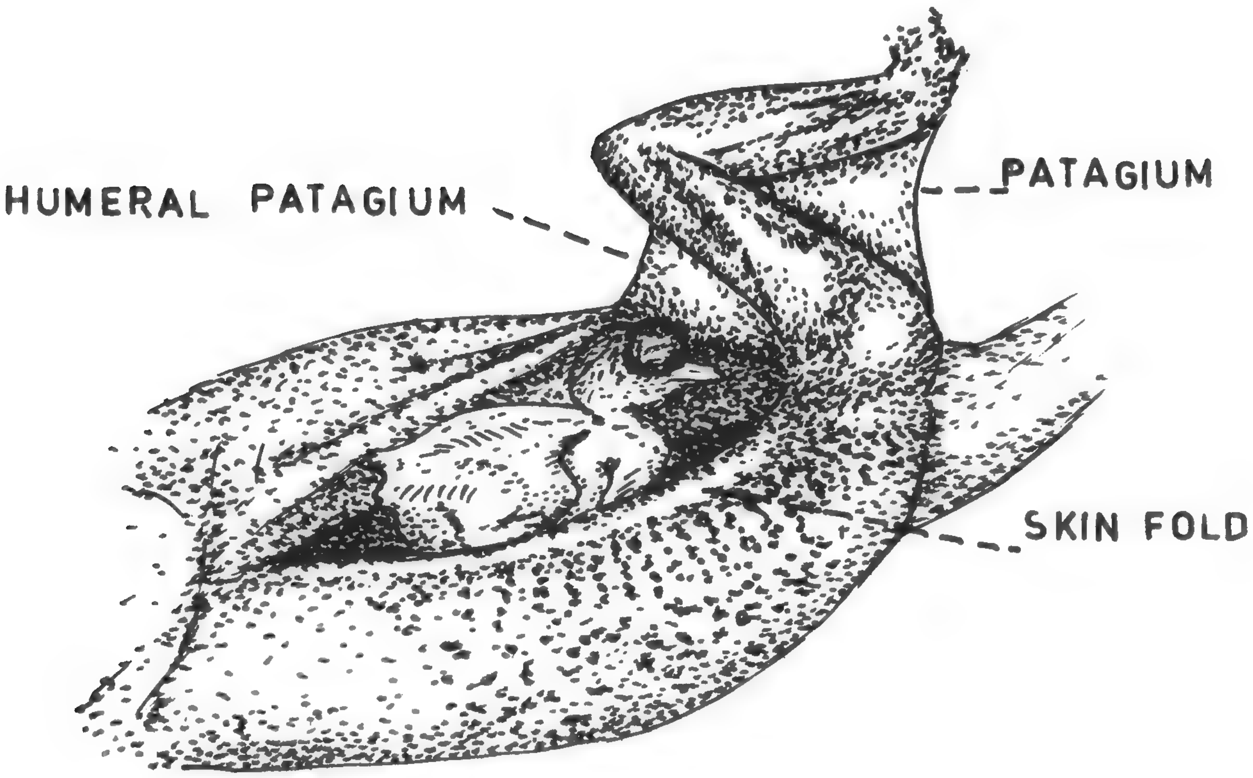
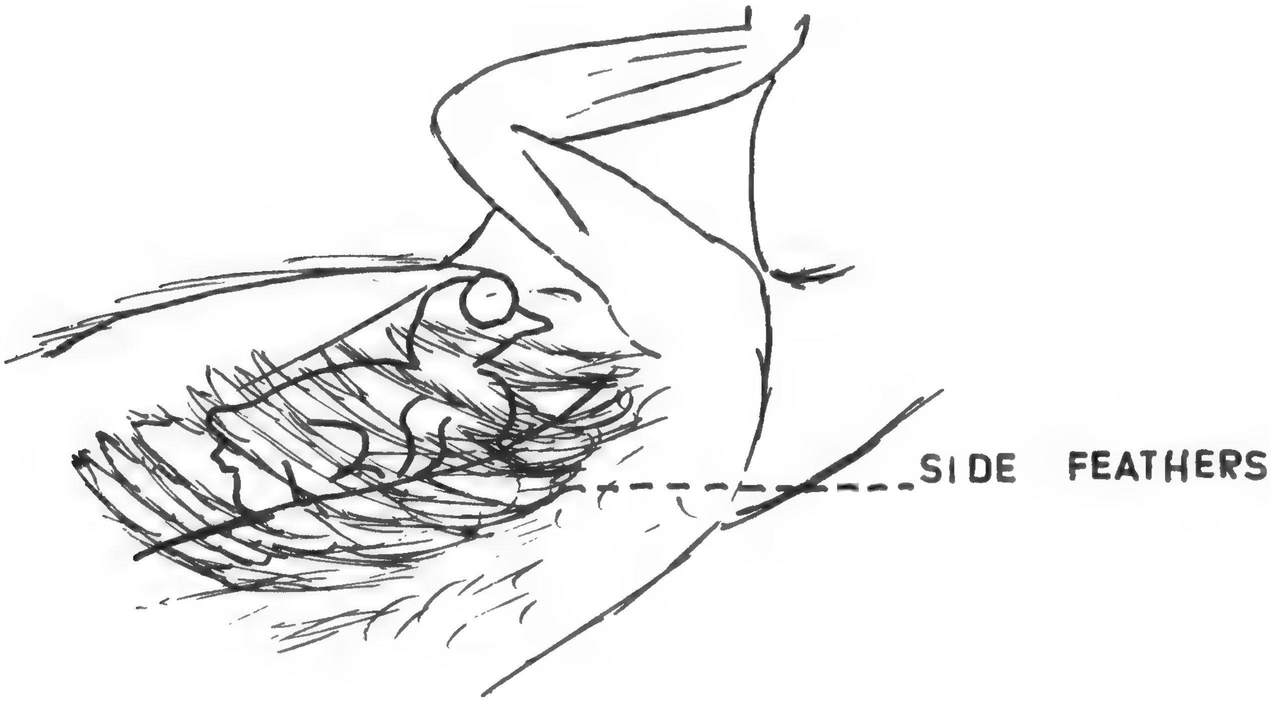


Figure 4 (*above*). A sketch, drawn from a specimen, shows the location of the shallow brood pocket and the position of the chick in the fold against the side of the male's body beneath the wing. Illustrations drawn by the author.

Figure 5 (*below*). The feathers of the side project upward, enclosing the chick in the pocket so that only the head protrudes. These feathers play an important role in providing warmth as well as helping to keep the chick securely in the pocket.



Although the incubation period was short, I believed, because of the eggshells, that the hatching had been normal and that the chicks were hidden somewhere.

I moved away from the nest to hide and wait. Soon the male swam back and very cautiously climbed up the vines and into the nest. If the chicks were hiding, he gave no calls to bring them to him and I still saw no sign of them. In a little while, I again moved closer, and the finfoot once more dropped to the water and headed for the opposite shore. When I drew back a second time, the bird again returned to the nest.

Intrigued and confused by the bird's behavior, I withdrew again and engaged a man with a little fishing boat to help me. As he approached the nest in his boat, I waited upstream. The bird jumped off the nest and, by lucky chance, swam upstream toward me, coming to land some 20 meters beyond me. Then, seeing me so close, he flew. As I watched the bird in flight through binoculars, I saw two tiny heads sticking out from the plumage of the sides under the wings. The finfoot had his chicks with him.

Subsequently, I collected the male and discovered that he had a special mechanism for carrying the young (Figures 4 and 5). On either side, beneath the wing, a pleat of skin forms a slight depression or cavity into which the young fit — one under each wing. Numerous side feathers, which enclose the body of the chick, add to the effectiveness of this "pocket." Muscular control probably holds the chick against the body, offering it warmth as well as concealment (Figure 6). In this depression the chicks are perfectly secure even when the male swims or flies. The female has no skin pleats under her wings and probably does not care for the chicks, at least in the early period following hatching.

The chick, at hatching, is very undeveloped (Figure 7) — almost naked with pale pink skin. It measures 50 mm from bill tip to vent. Its eyes are large with tightly joined lids; its bill is short and soft with an egg-tooth. Its feet are plump and poorly formed. Its plumage consists only of short, sparse down in the capital, spinal, humeral, ventral, femoral, and caudal feather tracts. The down on the head, submalar area, and ventral neck is whitish; on the remaining feather tracts, it is dark gray. The spinal feather tract divides into two branches with a wide apterium the length of the back. I noted only vestiges of primary and secondary wing feathers.

Considering the helplessness and undeveloped state of the chicks at hatching, I believe that the male probably puts them immediately into the pockets beneath his wings — in some unknown manner — and keeps them there for a number of days — until they attain a degree of plumage and muscular development that allows them to accompany the parent under their own power with relative safety. While carrying the young, the male reaches beneath the wing to feed them and remove the droppings.

Except when disturbed, the male remained on the nest during the first day of hatching. On the second day, he left the nest site, taking the young with him.

The finfoot's short incubation period accounts for this unusual habit of transporting and caring for the young. I found the nest with the single egg on the afternoon of 15 April. The following morning, after the female left the nest at 09:00, I noted two eggs. If the female laid the second egg shortly after she arrived at the nest on the afternoon of 15 April, then incubation lasted 11 days. If, on the other hand, she laid the second egg early

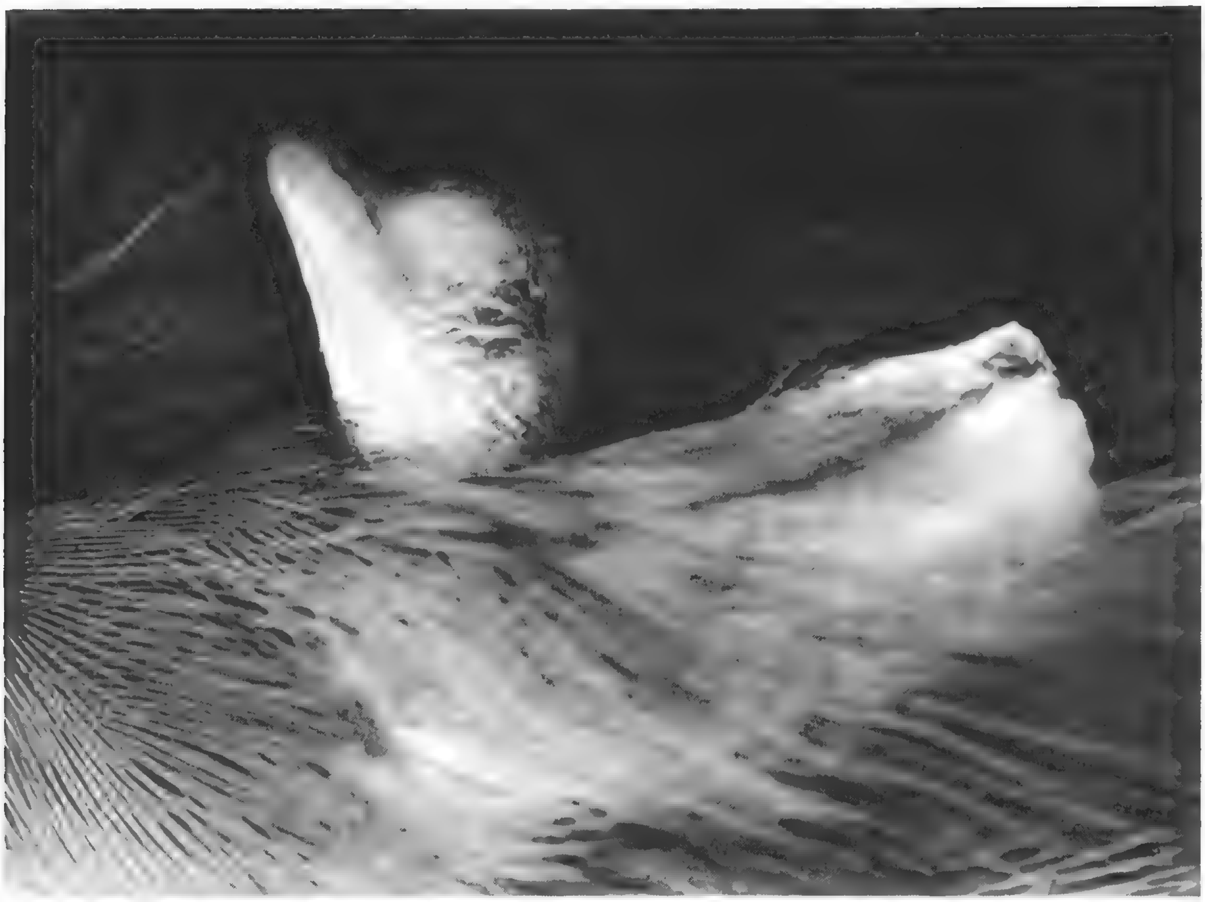
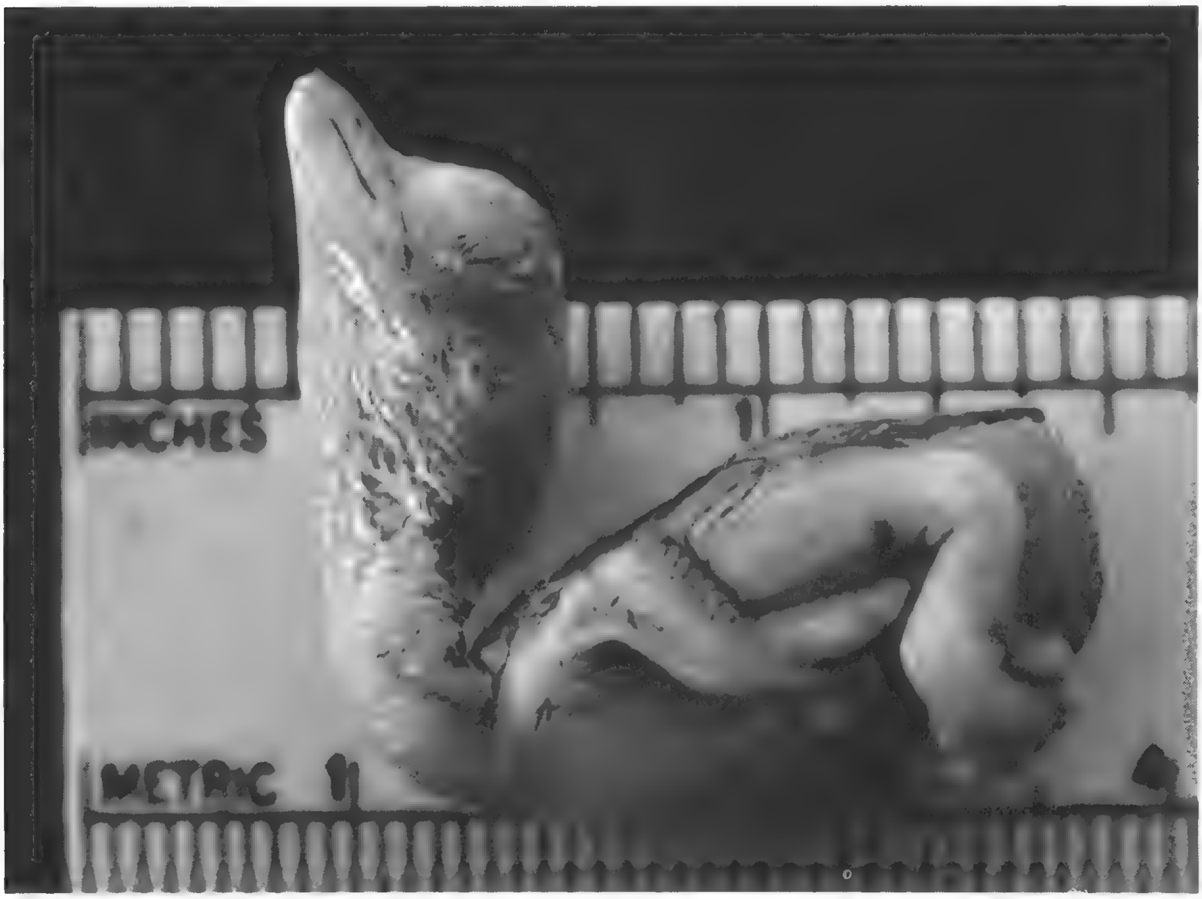


Figure 6 (*above*). The newly hatched chick, supported in the shallow pocket formed by a fold of skin and feathers of the side beneath the wing.

Figure 7 (*below*). The newly hatched chick is helpless, unable to see or to use its poorly formed legs. Only sparse, short down covers parts of the body.



on the morning of 16 April, the birds incubated for only 10.5 days, perhaps as little as 10 days and eight hours.

After hearing of my discovery of the finfoot's unique method of carrying its young, Dr. Alexander Wetmore kindly sent me a copy of several pages from a publication, in which the author (Wied, 1833) told of a male finfoot carrying his young in the manner described above. I believe that my observations are the first to confirm Wied's statements made over 100 years ago.

We have much more to learn about the biology of this tropical bird. So many questions arise: For instance, how long does the adult normally stay with the chicks on the nest? How does he put the chicks into the pockets? How long does he carry them with him? And what part does the female play during the hatching and post-hatching phase of the breeding cycle?

Summary

I observed the American Finfoot (*Heliornis fulica*) in southern Mexico over a period of two years. This species inhabits sluggish streams and rivers with densely vegetated margins and the edges of lakes. It lives solitarily, and each male appears to maintain his territory throughout the year, defending it with a circling display on the water. Courtship occurs toward the end of February. After pairing, the female assists in defending the territory. Both members of the pair construct the nest, a platform of sticks lined with leaves, in a tangle of dense vegetation over water. The female lays two eggs, and both sexes share the incubation which lasts from 10.5 to 11 days. The female is attentive from late afternoon until mid-morning the following day; the male incubates during the day.

The chicks are naked and helpless when hatched. The male places each chick under a wing in a "pocket," formed by a pleat of skin and feathers. In the nest that I observed, the male left the nest with the chicks in the pockets the day after hatching, but he probably kept the young in the pockets and fed them there until they had gained some independence.

My observations are the first to confirm the statements, made by Wied in 1833, concerning the carrying of young by the finfoot.

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OVERLAP IN THE DIET OF SOME NEOTROPICAL BIRDS

Charles F. Leck

When one considers the ecology of tropical birds and tries to test a number of hypotheses concerning the overlap of diet and the competition for food resources, he finds little on how many species and how many individuals feed at certain plants in certain ways. With this paucity of information in mind, I concentrated on the feeding habits of fruit- and nectar-eating birds at specific food sources, such as trees and shrubs, in Panama.

The goals of my study included (1) estimates of diet overlap and feeding specializations in the fruit-eating birds, or frugivores, in relation to the breadth of their niches, and (2) direct measures of the diet diversity of nectar-feeding birds over a three-month period. I measured the overlap of the frugivores in terms of foraging habits, feeding periods, size of food items, and species of food plant.

Study Area and Methods

Except where indicated, I collected all of the data from September 1968 through April 1969 on Barro Colorado Island, Canal Zone. The vegetation of this island is essentially mature, lowland rain forest (Beard, 1944) with a small clearing about the field station of the Smithsonian Tropical Institute (Eisenmann, 1952). In a previous publication (Leck, 1970), I summarized briefly the studies of many authors on the vegetation, fruit and flower phenology, and the climate of the island. I chose the clearing around the field station because, from it, I could frequently view the entire crowns of feeding trees, observe several resources in rapid succession, and identify and follow color-marked birds easily.

I observed the birds feeding at two widely distributed food plants, a mistletoe (*Oryctanthus occidentalis*) and a second-growth tree (*Cecropia* sp.), for 100 hours each, dividing the hours equally through the day in the following pattern: 06:30 to 07:00, 07:30 to 12:00, and 12:30 to 17:30. I noted in detail each visit of every species feeding at these plants — the arrival time, foraging height, and social behavior. I shall discuss the social behavior in another paper. In addition, I kept records of all fruit-feeding birds — the tanagers, flycatchers, and honeycreepers — and the nectar-feeding birds — the hummingbirds and honeycreepers — that fed on the 15 species of fruiting plants and 19 sources of nectar within the clearing.

The appendix to this article gives the scientific names of the birds mentioned in the text and tables.

Results and Discussion

The interspecific overlap in the fruit diets of many species, especially the closely related species, is most striking. The tendency of many species to travel about in mixed flocks means that many species feed together, increasing the frequency of diet overlap. Ten or more species may feed together regularly at an individual fruit tree or shrub. In one week, Beebe (1916) listed 51 species of birds, six of them manakins (Pipridae), entering a single fruit tree to feed. Willis (1966) listed 28 species, 15 of them tanagers, feeding on the berries of one species of shrub. From the more detailed observations of birds feeding at a variety of tropical plants, it is clear that a high diversity of exploiting species is probably common. Even birds, generally considered solitary, may feed in sizeable groups at favorable trees. Land (1963) observed Black-cheeked Woodpeckers feeding in aggregations of a dozen or more individuals at a *Miconia* fruit tree.

Having established the general pattern of many birds feeding in the same tree, we then want to know whether the different species are using the food resources of that tree in a "similar manner." If there is no significant difference in the feeding patterns of the different species in the tree, then we must go further and try to evaluate the degree of overlap in relation to their entire diets.

Feeding Heights

MacArthur (1958) was one of the first to show quantitatively how insectivorous species specialize in their use of a given food resource and avoid or reduce competition by feeding in different ways and at different sites. For instance, he observed the foraging behavior of several species of warblers in the same tree and found that each species had a specific feeding pattern. The differences in the hunting methods and feeding zones actually bring the warblers in contact with different foods and permit them to forage together on the breeding ground without interspecific competition. He also observed that the warblers retain their specialized methods of foraging on the wintering grounds in Costa Rica. Recent studies support MacArthur's findings, and Balda (1969) recorded this same division for other species of insectivores.

I watched for any similar ecological divisions in the niches of both insectivores and frugivores foraging in fruit trees and compared the differences in specialization between the two groups.

For the insect-eaters, I observed foraging heights and feeding methods of three species of warblers, the Tennessee, the Slate-throated Redstart, and the Wilson's. Because I made observations on the fruit-eaters at the tree at the same time, I could only record the gross divisions in the warblers' feeding methods. Specifically, I noted their foraging times in five different levels of the tree. The results in Table 1 show behavioral differences in their foraging patterns and suggest that these differences can effectively reduce competition between the three species. Of course, a more refined examination of the foraging — such as considering central and peripheral locations whether close to the trunk or out on a branch — might show even more differences. Since the vegetational and structural complexity of tropical trees offers insectivores, such as warblers, so many specialized feeding sites (Atkinson, 1966), it is not surprising that many species can share an individual tree with little or no competition.

My study of the fruit-eating birds in the tree (Table 2) revealed much less layering of foraging heights than occurred with the insectivores. At most, some species — for example, the Red-eyed Vireo — avoided the lower portion of the tree while other species — such as the Variable Seedeater — avoided the upper portion. This slight layering seems to be consistent with the normal foraging heights of these two species when searching for other foods in other areas. That is, the Red-eyed Vireo, an opportunistic feeder that also

TABLE 1

Foraging Behavior of Three Warblers in a Tree* near Cerro Punta in the Mountains of Western Panama at 5,900 Feet

Species	*Number of feeding visits*	*Foraging heights†*					*Foraging methods*
		Top	*Upper middle*	*Lower middle*	*Bottom*	*Trunk*	
Tennessee Warbler	10	53	47				Searching along branches.
		135	120				
Slate-throated Redstart	5	5	45	40	5	5	Frequent sallies for insects in flycatcher fashion.
		30	300	270	30	30	
Wilson's Warbler	25	5	26	33	20	16	Hunting along branches and among epiphytes on trunk.
		40	235	297	183	145	

*Total height 60 feet; crown about 30 feet high by 15 feet in diameter. Data gathered in 1968: 9 March, 07:00–11:00; 11 March, 15:00–16:30; 15 March, 16:30–18:00; 22 March 07:00–11:00.

†Upper figure gives per cent of total time in feeding zone; lower figure gives the time in seconds.

eats insects, most often forages for them in the canopies of trees. The Variable Seedeater, also an opportunistic feeder, most often searches for seeds on the ground or in the low vegetation. These two species merely fed in their normal areas.

Of the other low fruit-feeders at the tree, the Ochre-bellied Flycatcher normally forages for insects close to the ground (Slud, 1964); of the "high" feeders, the little-known Sulphur-rumped Tanager seems to be a canopy species everywhere (Eisenmann, 1952). The fruit-feeding heights of such species are then directly related to their heights when feeding on non-fruit items—the seeds, insects, etc.

Diamond and Terborgh (1967) reported similar feeding distributions in a fruit tree in Peru: the high feeders included a toucan (*Ramphastos* sp.) and a honeycreeper (*Dacnis* sp.); the low feeders were the trogons (*Trogon* spp.). If we consider the non-fruit diets of these species, we find that the toucan takes small lizards basking in the sun on the upper branches of trees and the eggs and young of birds nesting in tree crowns; the honeycreeper takes nectar and insects from the flowers of the canopy; and the trogons take katydids and other orthopterans from the lower vegetation. Again it appears that any layering of a tree for fruit-feeding might be directly related to the usual behavior of the species when feeding on non-fruit items.

And by the same token, the feeding *methods* of a species feeding on fruits are the same as its methods when feeding on non-fruits. For example, flycatchers, manakins, and trogons often take berries in flight in the same way they capture insects; vireos and woodpeckers eat their fruit while perched just as they eat insects (Leck, 1969). There are exceptions, of course, but in general this principle applies to most species.

Whatever the basis of the feeding levels at fruit trees, it does not seem that the layering reduces the competition for fruits as suggested by Diamond and Terborgh (1967) who cite MacArthur (1958). We must remember that insect-eaters reduce competition not only by using different layers of a tree, but also by using different feeding behaviors, all of which permit each individual species to exploit a somewhat different insect resource. Clearly, this cannot be the case with the fruit-eaters. A tree has one resource for the fruit-eaters and many different resources for the insect-eaters. Whether a species takes a berry on the wing or while perched makes no difference as far as competition is concerned, and whether the bird eats fruit high or low in a tree makes little difference, as the resource, the fruit, is the same.

Even if one argues that the resource on a given fruit tree may not be the same throughout because the fruit in one part may ripen before the fruit in another, we can assume that the preferred fruit is the same because most birds select ripe fruit. The defensive systems of unripe fruits — the hard pericarps and repugnant fluids — make it unpalatable for most birds. Furthermore, ripe fruit is usually conspicuous, and if it is scarce at a species' usual foraging level, the bird can easily move up or down, or in or out, to forage effectively.

TABLE 2

Foraging Behavior of Eight Fruit-eating Birds in a Tree with *Oryctanthus* Berries* at Barro Colorado Island from September to November 1968

Species	*Number of feeding visits*	*Zone of the tree†*		
		Top	*Middle*	*Bottom*
Short-billed Pigeon	87	*32*	*46*	22
		38	40	19
Social Flycatcher	133	*33*	*38*	29
		44	50	39
Paltry Tyrannulet	75	32	*43*	25
		24	32	19
Ochre-bellied Flycatcher	148	21	*37*	*42*
		31	55	62
Red-eyed Vireo	44	*36*	*43*	21
		16	19	9
Golden-masked Tanager	57	17	*46*	*37*
		10	26	21
Sulphur-rumped Tanager	98	*42*	*37*	21
		41	37	20
Variable Seedeater	46	20	*43*	*37*
		9	20	17

*A parasitic mistletoe growing throughout a *Persea americana* tree.

†Upper figure represents the percentage of total time in zone; lower figure gives time in seconds; percentages in italics denote the most frequented areas for each species.

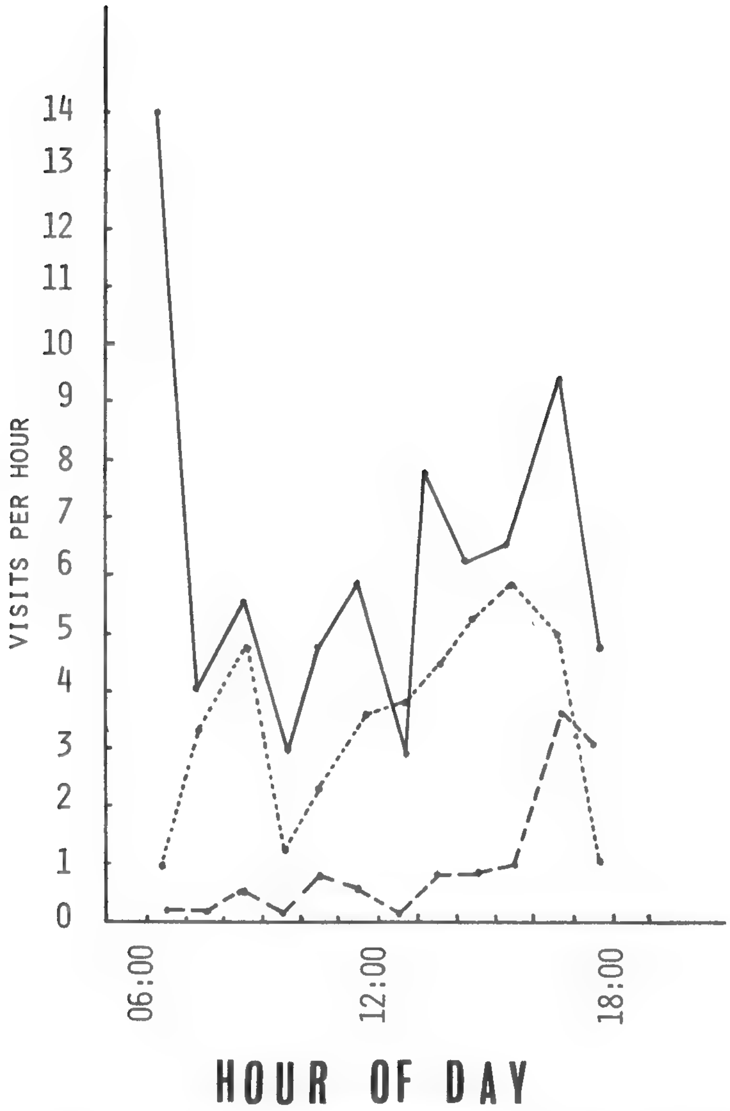

Figure 1. Visits per hour to a *Cecropia* tree by three of the more common fruit-eating birds, based on 101 hours of observation from September to November 1968 at the clearing on Barro Colorado Island. Solid line represents Plain-colored Tanager; dotted line, Blue-gray Tanager; dashed line, Collared Aracari.

Unfortunately, I collected little data on such movement between layers or layer expansion. I did note that the common Blue-gray Tanagers and Palm Tanagers, both of which usually forage well above two meters, fed on weed fruits within a foot of the ground during a food shortage in the wet season.

Temporal Patterns

Feeding periods for specific species may sometimes divide a food resource and competition at different levels, particularly if the resource, like nectar, is rapidly renewed. For example, nectar-feeding insects cut down competition by spacing the time of their visits to flowers because the plants rapidly replenish the supply of nectar after each feeding period (Linsley, MacSwain, and Raven, 1963). With a non-renewable, short-term resource, such as fruit, where the supply is limited and replenished very slowly, if at all, such divisions of time are unlikely to reduce competition effectively. Any fruits taken in the early part of the day are gone — just gone — clearly unavailable and irreplaceable. This may even apply to a nectar source if the morning feeding by many hummingbirds is intense enough to exhaust the tree's supply for the afternoon (see Stiles and Wolf, 1970).

An exception to this might be a tree where the fruits in different stages of ripeness are ripening very rapidly — a situation that rarely occurs in the tropics.

It is particularly improbable that fruit could ripen fast enough to replace the exploited fruit by freshly ripened fruit within several hours. Hence, I predicted that, unlike nectar-feeders, most frugivores would feed on fruits throughout the day and that any divisions of time according to species would be insignificant in reducing competition at fruiting trees. My observations at the *Cecropia* trees verified this prediction. Figure 1 shows that the feeding times overlapped greatly although certain species sometimes had characteristic peaks in the early morning or late afternoon.

Similarly, at the *Oryctanthus* plants birds fed on berries throughout the day, and closely related species often fed at the same time (Figure 2). In these and other trees, the total rates of exploitation for all frugivorous species were usually greatest in the early morning from 06:30 to 08:00. Earlier (Leck, 1969) I wrote: this "pattern of early feeding may simply reflect a physiological need to eat as soon as activities are undertaken in the morning, and a general avoidance of activity during the warmer hours of the day."

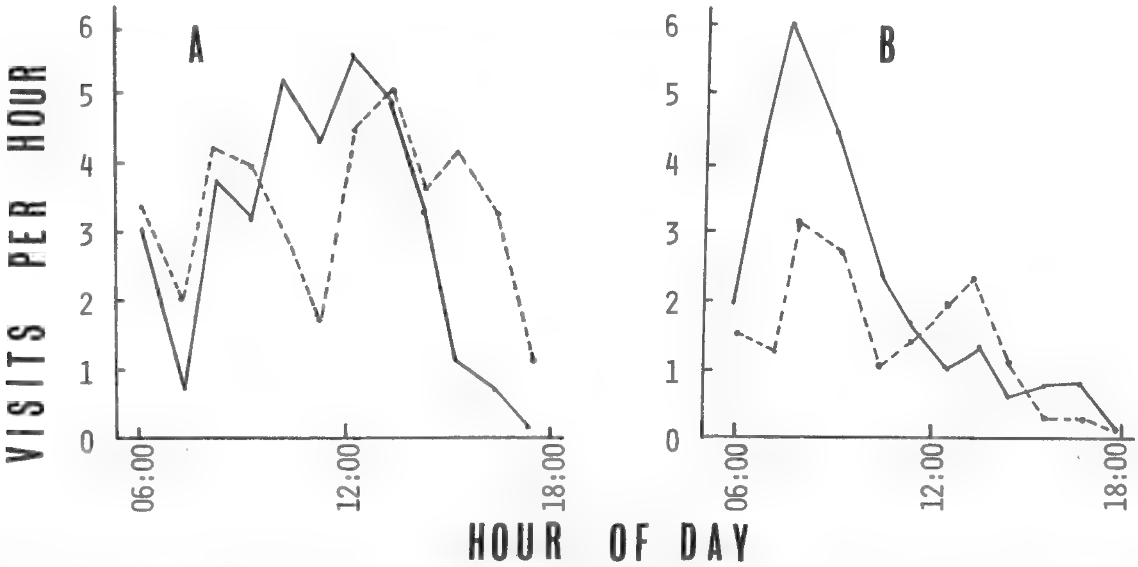

Figure 2. Visits per hour to mistletoe plants (*Oryctanthus*) by two flycatchers and two tanagers, all common fruit-eating species, based on 101 hours of observation from September to November 1968 at the clearing on Barro Colorado Island. (A) Solid line represents Social Flycatcher; dashed line represents Ochre-bellied Flycatcher. (B) Solid line represents Sulphur-rumped Tanager; dashed line represents Golden-masked Tanager.

Size of Food Item

Finally, each bird species might divide the fruit resources as a whole by specializing in fruits within a particular size range. Betts (1955) showed that a number of insectivorous species of birds divide the food resources according to a modal size and that the patterns of such divisions are closely correlated with differences in beak structure. Bowman (1961) provided detailed anatomical information showing the relationship between bill structure and diets of both fruit- and insect-eating finches. Later, Schoener (1965) showed that the bill differences — within culmen lengths — among members of frugivorous families are usually very small as compared with differences among members of insectivorous families, particularly in the tropics. He based his analysis on sympatric congeneric species — on species in the same genus living in the

TABLE 3

Fruit Items in the Diets of Seven Flycatchers*

Mean culmen length	*Species*	*Plant species† and diameter of berry (mm)*					
		P.3††	*O.3*	*L.5*	*H.5*	*D.7*	*T.8*
Large > 21 mm	Boat-billed Flycatcher				x	x	
	Streaked Flycatcher		x	x			
	Tropical Kingbird			x	x	x	x
Medium = 15 mm	Social Flycatcher	x	X		x		x
Small < 12 mm	Ochre-bellied Flycatcher		X				
	Paltry Tyrannulet	x	X				
	Yellow-crowned Tyrannulet	x	X				

*Data collected in clearing on Barro Colorado Island from September 1968 through April 1969.

†Major food item = X; minor food item = x.

††*P.* = *Phoradendron, O.* = *Oryctanthus, L.* = *Lantana, H.* = *Hamelia, D.* = *Didymopanax, T.* = *Tetracera.*

same area. The very small interspecific differences in the bills of fruit-eating species suggest that they do not divide the food resources according to the size of the fruit, a supposition supported also by the feeding overlap of many species at one fruit tree.

Schoener (1965:112) summarized the ecological reasons why such partitioning might generally not be feasible for fruit-eaters and concluded: ". . . where a large number of potentially competing species occurs . . . rather than evolve the precise perceptual mechanisms necessary for discriminating small food size spans, species will consistently avoid competition by evolving differences in feeding habitat or foraging behavior . . ." In other words, it is "cheaper" for a species to develop adaptations for a new food or method of feeding than it is to develop ways of distinguishing small fruits from large. I should emphasize, however, that a single dimension — such as culmen length — is often an inadequate measure of bill specialization (Root, 1967). Furthermore, food partitioning itself is not usually based on a single factor, such as food size, but involves numerous specializations for foraging — for example, morphological adaptations of the feet to particular perch sizes (Root, 1967; Willis, 1967). These additional parameters require a much more detailed behavioral study than I made. Thus, I shall consider only briefly the relationship between the size of the bills and the ranges in size of fruits in the diets of the frugivores. With such limitations, and with the culmen length as an indicator of food size in mind, the analysis provides some interesting results.

In the field, it is obvious that certain small-billed birds cannot feed on some large fruits, particularly those with hard pericarps and tough texture.

TABLE 4

Fruit Items in the Diets of Three Common Tanagers*

Mean culmen length	*Species*	*Plant species† and approximate size of fruit (mm)*											
		Po.††	*P.m.*	*P.l.*	*Ph.3*	*O.3*	*T.3*	*L.5*	*I.5*	*H.5*	*D.5*	*C.*	*M.*
			narrow catkins									*large*	
Large > 12 mm	Blue-Gray Tanager		x							X	x	X	
	Palm Tanager		x							X	x	X	x
Medium = 10 mm	Golden-masked Tanager				x	X							
Small < 9 mm	Plain-colored Tanager	x		x	x		X	X	x	X	x	X	
	Fulvous-vented Euphonia	X	X	X	x			X		x		x	

*Data collected in clearing on Barro Colorado Island from September 1968 through April 1969.

†Major food item = X; minor food item = x.

††*Po.* = *Pothomorphe, P.m.* = *Piper marginatum, P.l.* = *Piper leptocladum, Ph.* = *Phoradendron, O.* = *Oryctanthus, T.* = *Tetracera, L.* = *Lantana, I.* = *Isertia, H.* = *Hamelia, D.* = *Didymopanax, C.* = *Cecropia, M.* = *Musa.*

Birds with larger bills, however, seem to have no lower limit to the size of the berries on which they can feed easily. For instance, the Crested Guan and *Ramphastos* toucans regularly take berries of the *Didymopanax* that are only seven millimeters in diameter. The situation of the frugivores parallels that of the insectivores, according to Schoener and Janzen (1968), where ". . . small predators rarely take very large food, large predators often feed on quite small prey."

More significant than size were the types of food preferred by the flycatchers and tanagers in the clearing at Barro Colorado. These foods appeared to be related to bill size. The larger-billed flycatchers generally took larger berries than did the smaller-billed flycatchers (Table 3). Actually, the flycatchers, because of the great differences in the size of the bills of various species — from 12 to 21 mm — that reflect their specializations for insect feeding, are adapted for the partitioning of fruit by size.

The tanagers show a relatively small range of bill sizes — from 9 to 12 mm. They are also less apt to take larger or smaller berries on a basis of bill size (Table 4). For instance, the larger berries are the major food items for the Plain-colored Tanager, a bird with a small bill.

Table 4 reveals that the tanagers with the greatest overlap in their diets were those with similar bill lengths — the Fulvous-vented Euphonia and Plain-colored Tanager, the Blue-gray Tanager and Palm Tanager. According to Terborgh and Diamond (1970), differences in bill size or body size may limit the diets of fruit-eating birds, particularly the opportunistic species that also feed on insects. Nevertheless, I found diet overlap in almost all of the species I studied, and the extent of overlap was considerable in closely related species. Hence, if the fruit resources are limited, some other modifications in foraging behaviors must reduce the competition.

Diet Overlap in Nectar Feeders

At Barro Colorado Island, flowers were less abundant at the end of the rainy season in November than during the dry season from December to February; and the nectar-feeding birds, the hummingbirds and coerebids, were also less common at the end of the rainy season than during the dry season (Leck, 1970). But even though the number of nectar-feeding species was much lower in the wet season, there appeared to be a shortage of nectar sources in the clearing for those that remained. For example, each morning in mid-November at least eight Violet-bellied Hummingbirds visited one of the few *Hamelia* shrubs in flower, arriving well before sunrise at 06:12. They displayed aggressively at this shrub, with frequent supplanting attacks and pursuit-flights, behaviors indicating competition for nectar (Stiles and Wolf, 1970). One could easily observe 30 or more attacks within half an hour. In the dry season, when there were many more birds and many more flowers, competition was greatly reduced.

During the first three months of the dry season, December, January, and February, I kept daily records of all hummingbirds and their food flowers as they appeared during general censusing or during my observation periods at the flowering trees. I found that the hummingbirds' diets shifted monthly with the flowering periods of their major food plants, just as Wolfe (1970) reported from Costa Rica. The diet records of the hummingbirds (Tables 5, 6, and 7) show that, though some overlap occurs, most every species has its preferred flowers. The two exceptions — where two species of hummingbirds

TABLE 5

Hummingbird Diets in the Clearing on Barro Colorado Island in January 1969

Species	*Food plants**												
	Di.†	*Ma.*	*Ps.*	*Hi.*	*He.*	*Ca.*	*Ha.*	*Is.*	*Tr.*	*Qu.*	*La.*	*Oc.*	*Cl.*
Purple-crowned Fairy	1	2	3										
White-necked Jacobin			5	3	4				2			1	
Crowned Wood-Nymph				2	1	6	3	5				4	
Rufous-tailed Hummingbird				5			2	1	4				3
Violet-bellied Hummingbird							1		2				
Long-tailed Hermit										1			
Rufous-crowned Coquette									1		2		

*Numbered in decreasing order of importance, based on frequency of visits.

†*Di.* = *Cioclea, Ma.* = *Manihut, Ps.* = *Psidium, Hi.* = *Hibiscus, He.* = *Heliconia, Ca.* = *Caesalpinia, Ha.* = *Hamelia, Is.* = *Isertia, Tr.* = *Trichlospermum, Qu.* = *Quassia, La.* = *Lantana, Oc.* = *Ochroma, Cl.* = *Clerodendron.*

TABLE 6

Hummingbird Diets in the Clearing on Barro Colorado Island in February 1969

Species	*Food plants**									
	Hi.†	*He.*	*Ha.*	*La.*	*Oc.*	*Cl.*	*Ta.*	*Mc.*	*Ix.*	*Ja.*
Purple-crowned Fairy							1			
White-necked Jacobin					3			2		1
Common Wood-Nymph	2	1								
Rufous-tailed Hummingbird	7	3	1	5		6			4	2
Violet-bellied Hummingbird			3	1					2	
Long-tailed Hermit	1									
Rufous-crowned Coquette									2	1

*Numbered in decreasing order of importance, based on frequency of visits.

†Abbreviations the same as in Table 5, plus *Ta.* = *Tabebuia, Mc.* = *Macronemum, Ix.* = *Ixora, Ja.* = *Jacaranda.*

TABLE 7

Hummingbird Diets in the Clearing on Barro Colorado Island in March 1969

Species	*Food plants**										
	Hi.†	*He.*	*Ha.*	*La.*	*Oc.*	*Cl.*	*Ta.*	*Ix.*	*Ja.*	*Pa.*	*Sp.*
White-necked Jacobin	4				1	3			2		
Common Wood-Nymph	1	2									
Rufous-tailed Hummingbird	3	5	1	4				2			6
Violet-bellied Hummingbird					2			1		3	
Long-tailed Hermit	1	2									
Black-throated Mango							1	2			

*Numbered in decreasing order of importance, based on frequency of visits.

†Abbreviations the same as in Tables 5 and 6, plus *Pa.* = *Papilionata* sp., *Sp.* = *Spathodea.*

visited the same plant most frequently — provided many cases of supplanting attacks. In fact, several birds established feeding territories which they defended vigorously. The tables also show that the species that visited the fewest flower species each month were the morphological extremes — the large Long-tailed Hermit and the tiny Rufous-crested Coquette. For the three months, the diet diversities increased in three species, decreased in three species, and remained the same in three species.

Although one might expect a correlation between bill size and the length of the corolla tube of the flower, I found none (Table 8). Several factors may account for this: (1) The flowers varied a great deal in ways other than the size of the corolla. (2) In the wet season, the nectar-feeders reduced competition by emigration rather than by diet specialization. (3) In the dry season, flowers were so abundant that there was no evident competition. (4) The size of the corolla tube has no effect on species, such as coerebids, that sometimes obtain their nectar by making holes in the base of the corolla tube (Skutch, 1964), or on species that feed at holes made by other species. In a group of closely related sympatric plants, of limited abundance and with flowers so thick that the birds could not pierce the corolla, a correlation between bill length and flower size would be much more likely. In fact, this does seem to be the case with the flowers of the *Heliconia* spp. and their hummingbird pollinators in certain areas of Costa Rica (Richard Mack, pers. commun.).

I also recorded the diets of the coerebids through both the wet and dry seasons (Table 9). In the wet season, the Bananaquit was the only coerebid present regularly, and it dominated — i.e., it was the supplanting species — in interactions with hummingbirds at the few nectar sources.

In the dry season, when more fruit and flowers were available, the other coerebids showed up. Although their diets all overlapped the diets of the hummingbirds, there was so much more food in the clearing that competition was not significant.

TABLE 8

Bill Length of Humming-birds versus Food-plant Flower Size

Species	*Bill length (cm)*	*Food plants**																	
		La.†	*Pa.*	*Ma.*	*Ix.*	*Ha.*	*Tr.*	*Cl.*	*Ca.*	*Ps.*	*He.*	*Di.*	*Hi.*	*Is.*	*Ja.*	*Sp.*	*Qu.*	*Ta.*	*Oc.*
Long-tailed Hermit	4.1										x		x				x		
Common Wood-Nymph Black-throated Mango	2.3		x		x	x			x		x		x	x				x	
White-necked Jacobin Rufous-tailed Hummingbird	2.0	x		x			x	x		x	x		x	x	x	x		x	x
Purple-crowned Fairy Violet-bellied Hummingbird	1.5	x				x	x			x		x						x	
Rufous-crowned Coquette	1.0	x		x			x								x				

*Data collected on Barro Colorado Island from February through March 1969.

†Listed in approximate order of size with the smallest on the left. Abbreviations as in Tables 5, 6, and 7.

TABLE 9

Diets of Honeycreepers in the Clearing on Barro Colorado Island, 1968–1969*

Species	*Nectar plants*†						*Fruit plants*							*Insects*
	Co.	*Ha.*	*Hi.*	*Ma.*	*Oc.*	*Ta.*	*Tr.*	*T.*	*Py.*	*Po.*	*L.*	*H.*	*C.*	
Bananaquit	X	X	X			X								
Blue Dacnis	X			X		x	X	X		X	X			x
Red-legged Honeycreeper	x				x	X	X	X						x
Green Honeycreeper							X		X		X	X	X	

*Plant abbreviations as in Tables 5, 6, and 7, plus *Co.* = *Cordia, Py.* = *Psychotria.*

†Major food item = X; minor food item = x.

Moynihan (1963) found similar examples of several sympatric species of coerebids sharing the flowers of the same plants and otherwise overlapping in their diets. He indicated that the ecological differences among such birds may involve habitat preferences or the relative amounts of fruit and insects in the diet. Note in Table 9 how the proportion of fruit in the diets of the coerebids ranges from none in the Bananaquit through approximately 30 per cent in the Red-legged Honeycreeper and 50 per cent in the Blue Dacnis to 80 per cent in the Green Honeycreeper. Among species with less flexible diets, we should expect the competition to be more frequent and severe when foods are not superabundant. Ripley (1959) found this to be the case with the sunbirds (Nectariniidae) of eastern Indonesia, which are more specialized than the coerebids.

Conclusion

The exploitation of representative fruiting plants showed species-specific specializations. Warblers, the insectivores, foraged to some extent at different levels — by layering — and exhibited other behavioral differences in their feeding. Frugivorous species foraged at all levels, and the slight layering that they did show was probably only a by-product of their non-fruit feeding habits. I consider that layering in general was an ineffective method of resource partitioning for the fruit-eaters. I also believe that the temporal separation of the feeding periods — one species feeding in the morning and another in the afternoon — was not significant.

The size of the food items was more important to diet diversity in the opportunistic frugivores — e.g., in the flycatchers that ate both fruit and insects — than to the obligate frugivores — e.g., the tanagers that ate only fruit. This difference was related to the range of bill sizes in the two groups. The opportunistic feeders had a greater range of bill size. In theory it is ecologically impractical to have many specialists partitioning fruit resources by size (Schoener, 1965).

Thus, if the supply of fruit is limited — and we have evidence that food shortages are a regular seasonal occurrence for much of the tropics (Leck, 1970) — then obligate feeders that exhibit much diet overlap and have few interspecific differences in feeding behavior will strongly compete for the available food. On the other hand, the opportunistic frugivores feeding at the same trees may escape much of the competitive pressure by switching to alternate foods whenever the supply of fruit is low. These species often partition the alternate food source, usually insects, by using different foraging patterns.

Hummingbirds, with few exceptions, showed species-specific food preferences that varied during the three months of observation; with two exceptions, the species did not overlap at their favorite flowers. The levels of aggressive behavior were high between the exceptions — where two species preferred to feed at the flowers of the same plant. Both diet specializations and resource territoriality suggest that a limited amount of nectar is available at some time in the annual cycle. I did not determine the basis of diet diversities. Bill size may be an important restriction particularly for the large and small species.

Coerebids should adapt well to fluctuations in food supply because their diets are broad and include nectar, fruit, and insects. Proportions of each food category varied with the species considered and no doubt also varied with the seasonal changes in the availability of certain foods. The variations in their diets permit many similar species to feed together without too much competition.

Summary

This paper is based, for the most part, on data collected at Barro Colorado Island, Canal Zone, for the purpose of determining the overlap in the diets of fruit- and nectar-feeding species that fed on 15 species of fruiting plants and 19 sources of nectar in and around a clearing.

In one tree the different species of warblers, all insect-feeders, layered their feeding areas — that is, fed at different heights with different behavior patterns and there was little competition between them.

The fruit-eating birds layered the tree very little. Each species fed, as a rule, at its normal feeding height but moved easily from high to low to medium — to wherever there was ripe fruit. The layering of the tree did not prevent the competition among them. Neither did they avoid competition by feeding at different times of the day. The peak of feeding for most species was early morning, and certain species had characteristic peaks in the afternoon.

The insignificant differences in bill size among the fruit-eating species, compared to the much greater differences in bill size among insect-feeders, suggest that the fruit-eating species do not partition the food according to the size of the fruit. Some of the birds with small bills could not manage the large fruits, but the birds with large bills ate fruits of all sizes. Thus, there was diet overlap among the birds with large and small bills. The fact that the fruit resource within a given tree does not change, as does the insect resource, suggests that the fruit-eaters must have some modifications in foraging behavior that prevent competition.

When there were few hummingbirds and few flowers, the diets must have overlapped because aggressive behavior was rampant. When there were many more species in bloom, there was less aggressive behavior. In spite of the fact that there were more hummingbirds, competition was less because each species could use its preferred flowers and there was less overlap in their diets. There was no correlation between bill size and corolla size.

When the Bananaquit was the only coerebid present and flowers were few, it dominated the hummingbirds. When there were many flowers and the other coerebids returned, the competition was less even though the diets still overlapped. The coerebids were flexible, opportunistic feeders, able to consume nectar, fruit, or insects. The proportions of these three foods varied with the species — and probably with the seasons. These variations enabled the similar species to feed together without too much competition.

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APPENDIX

Scientific names of bird species mentioned in the text and tables:

Family Cracidae, chachalacas, guans, and curassows
  Crested Guan (*Penelope purpurascens*)

Family Columbidae, pigeons and doves
  Short-billed Pigeon (*Columba nigrirostris*)

Family Trochilidae, hummingbirds
  Long-tailed Hermit (*Phaethornis superciliosus*)
  White-necked Jacobin (*Florisuga mellivora*)
  Black-throated Mango (*Anthracothorax nigricollis*)
  Rufous-crested Coquette (*Lophornis delattrei*)
  Common Woodnymph (*Thalurania furcata*)
  Violet-bellied Hummingbird (*Damophila julie*)
  Rufous-tailed Hummingbird (*Amazilia tzacatl*)
  Purple-crowned Fairy (*Heliothryx barroti*)

Family Ramphastidae, toucans
  Collared Aracari (*Pteroglossus torquatus*)
Family Picidae, woodpeckers
  Black-cheeked Woodpecker (*Centurus pucherani*)

Family Tyrannidae, flycatchers
  Tropical Kingbird (*Tyrannus melancholicus*)
  Streaked Flycatcher (*Myiodynastes maculatus*)
  Boat-billed Flycatcher (*Megarhynchus pitangua*)
  Social Flycatcher (*Myiozetetes similis*)
  Paltry Tyrannulet (*Tyranniscus vilissimus*)
  Yellow-crowned Tyrannulet (*Tyrannulus elatus*)
  Ochre-bellied Flycatcher (*Pipromorpha oleaginea*)

Family Vireonidae, vireos
  Red-eyed Vireo (*Vireo olivaceus*)

Family Coerebidae, honeycreepers
  Green Honeycreeper (*Chlorophanes spiza*)
  Red-legged Honeycreeper (*Cyanerpes cyaneus*)
  Blue Dacnis (*Dacnis cayana*)
  Bananaquit (*Coereba flaveola*)

Family Parulidae, wood warblers
  Tennessee Warbler (*Vermivora peregrina*)
  Wilson's Warbler (*Wilsonia pusilla*)
  Slate-throated Redstart (*Myioborus miniatus*)

Family Thraupidae, tanagers
  Fulvous-vented Euphonia (*Tanagra fulvicrissa*)
  Plain-colored Tanager (*Tangara inornata*)
  Golden-masked Tanager (*Tangara larvata*)
  Blue-gray Tanager (*Thraupis episcopus*)
  Palm Tanager (*Thraupis palmarum*)
  Sulphur-rumped Tanager (*Heterospingus rubrifrons*)

Family Fringillidae, finches and grosbeaks
  Variable Seedeater (*Sporophila aurita*)

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CLIFF-NESTING RAPTORS AND RAVENS ALONG THE COLVILLE RIVER IN ARCTIC ALASKA

Clayton M. White and Tom J. Cade
Photographs by the authors

North of the great Yukon River — beyond the last fingers of boreal forest extending along the south flowing drainages of the Brooks Range — lies a vast stretch of tundra familiarly called the Arctic Slope of Alaska. Some 80,000 square miles in extent, the Arctic Slope, though far from unscarred by modern man's activities, is a true wilderness — one of the last remaining within the territorial limits of the United States (Cade, 1970). Here the wolf still hunts the caribou as it has done for thousands of years; the wolverine and the barren ground grizzly still roam the countryside. In spring, tens of thousands of wild geese and ducks, a great variety and abundance of plovers and sandpipers, and many other arctic nesting birds arrive and join with the hardy, resident ptarmigan to breed during the continuous daylight of the brief summer. Here, too, the Peregrine Falcon, the Gyrfalcon, and the Rough-legged Hawk still scream defiance to intruders at numerous craggy aeries along the fast flowing arctic rivers in the northern foothills of the Brooks Range. The wily Raven—called "Tuluak" by the Nunamuit Eskimos—casts his black shadow across the faces of these same cliffs.

Kessel and Cade (1958) first called attention to the arctic river bluffs as important ecological formations for certain breeding birds in northern Alaska. Peregrines, Gyrfalcons, Rough-legged Hawks, and Ravens all nest side by side on the cliffs along the Colville River; all eat some of the same kinds of prey, and, in so doing, all use common resources of the environment. Thus, individuals of these four species are in frequent contact during the breeding season.

Birds with similar food and nesting requirements are potential competitors for resources that may be in short supply; but according to theory, competition tends to develop different specializations among ecologically similar species living in the same environment. The specializations that mitigate interspecific competition may involve morphological, physiological, or behavioral adjustments.

Because these four species are similar in habits and behavior, because they require a cliff-nesting habitat that appears to be a limited resource over which we might expect competition to occur, and because the variety of prey available to avian predators in the Arctic is small, thereby limiting opportunities for feeding specializations, we have tried to answer the following questions.

Do the falcons, hawks, and ravens use the cliffs in different ways when locating their nests? How does the timing of reproduction differ among the four species, and do these differences have any bearing on the occupancy of cliffs? How does the presence of a breeding pair of one species on a cliff attract or repel other conspecific pairs and the pairs of other species? Is there any evidence of mutually exclusive occupancy? To what extent do the four predatory species exploit the same species of prey? Do they use common prey populations in different ways or at different times? Do these four cliff-nesting species modify the environment to benefit one another in any significant way?

Those who are concerned about the current, rapid exploitation of the northern environment, and the damaging effect of man's activities there, often repeat the generality that the arctic ecosystem is fragile, simple, and unstable. Dunbar (1968) discussed all these ideas in his book, "Ecological Development in Polar Regions — A Study in Evolution," but one of his most salient points is that, in the geologically young environment of the Arctic, selection and evolution are "aimed" toward ecological stability. To us, ecological stability means that the seasonal and yearly changes in the numbers of individuals are not great enough to take any species into extinction, that the fluctuations in numbers tend to be around a more or less central position in time and space, that the numbers of no one species expand indefinitely at the expense of another because of the way it fills or occupies the habitat, and that the ecosystem maintains some kind of homeostasis, with continued energy input, in spite of the numerical oscillations of the species composing the system.

To achieve stability, organisms must be able to adapt and be successful while living side by side. Biological success is often measured by the ability of a species to leave the maximum number of progeny to the next generation. When species of similar behavior and ecology come together and occupy the same ranges, then the question of their abilities to make use of the environment in different ways becomes paramount for both stability and success. It is the broader question of how adaptation has allowed these four cliff-nesting species to live together sympatrically, to partition the environment, and to achieve ecological stability in the relatively simple ecosystem of arctic Alaska that we think gives relevance to our specific, analytical questions.

Characteristics of the Species

General Status and Distribution

All four species are wide-ranging with breeding populations that occur in major biotic communities (biomes) other than arctic tundra. Indeed, the Peregrine Falcon (*Falco peregrinus*) is a virtually cosmopolitan, polytypic species with numerous described subspecies (see Hickey and Anderson, 1969, for a recent summary). The Peregrines breeding in northern Alaska are a subspecies, *F. tundrius*, distinct from *F. p. pealei* and *F. p. anatum* (White, 1968a) and belong to a highly migratory population, the bulk of which winters south of the United States. As a species, the Common Raven (*Corvus corax*) is about equally as wide-ranging in the Northern Hemisphere as the Peregrine. The arctic Alaskan population of Ravens belongs to the subspecies *C. c. principalis*. The birds are large and resident the year round in northern Alaska. The other essentially resident arctic species, the Gyrfalcon (*Falco rusticolus*), is the largest of the true falcons. It breeds throughout the subarctic and arctic latitudes of both the Old and New Worlds and, of the four species, is the most narrowly restricted to northern environments. The common Rough-legged Hawk (*Buteo lagopus*) is also a bird of panboreal distribution with extensive breeding populations in the taiga and tundra regions of the Nearctic and Palaearctic (Cade, 1955). It migrates south of its breeding range in the winter, but not as far as the arctic Peregrines.

According to Johansen (1956), both the Gyrfalcon and the Rough-legged Hawk are true arctic species, having evolved under prevailing northern conditions. Presumably, their speciations and adaptive modifications were tied to climatic changes of the Pleistocene, and their ancestral stocks may have come from Asiatic grassland or steppe populations of large-sized falcons and buzzards. Peregrines and Ravens probably originated in mid-latitude regions, perhaps in the Old World and perhaps at an earlier time, and then spread northward into the Arctic.

Size

All four species, roughly similar in size, can be classed as medium-sized diurnal raptors, the Raven being a functional raptor. To many people either the wing length or weight indicates the size of a bird. We have used weights and wing measurements from the literature (Ridgway, 1904; Friedmann, 1950; Dement'ev and Gladkov, 1951; Brown and Amadon, 1968; and C. M. White, (1968b) to examine the relationship of "size" among these species. The results are presented in Table 1.

Male Ravens have the longest wings; male Peregrines, the shortest — the average for the Ravens being about 145 per cent longer than the average for the Peregrines with a progression of sizes between these extremes. Body weights give a somewhat different sequence. Female Gyrfalcons are the heaviest; male Peregrines, the lightest, with the difference approaching a factor of three.

As discussed by Brown and Amadon (1968), the real "size" of a raptor depends on both wing length and body weight. We consider the two together, the weight per unit area of wing, as the "wing-loading" of a bird. Without actually measuring the area of the wing, the relative wing-loading can be expressed by dividing the wing length from the wrist to the tip of the longest primary by the cube root of the body weight. This gives an index useful in comparing individual birds, species, or sexes. The lower the value, the more weight per unit area of wing length or the greater the wing loading. Again looking at Table 1, we see an interesting progression of differences among the males and females of our four Colville species with female Gyrfalcons having the heaviest wing-loading; male Rough-legs, the lightest. Perhaps the most significant indication of these figures is that all the falcons are grouped close together as forms possessing relatively heavy wing-loading, in keeping with their adaptations for fast, flapping flight, while the Ravens and Rough-legged Hawks have higher index figures, above 40, indicating significantly lighter wing-loading than for falcons, again in association with their greater reliance on soaring and gliding flight.

There is a marked difference in the size of the sexes in all species. Ravens follow the more usual rule among birds in that males average larger than females with the average wing length of males about 105 per cent longer than that of females, and the males about 127 per cent heavier. Males consequently have a heavier wing-loading than females. The falcons and Rough-legged Hawk follow the "falconiform rule" of reversed sexual dimorphism in size, females

TABLE 1

Differences in Various Characteristics of Size Among Four Species of Cliff-nesting Raptors on the Colville River

	Wing length			*Weight*			*Wing-loading**	
Species (largest to smallest)	*Sex*	*Mean wing length (mm)*	*Species (heaviest to lightest)*	*Sex*	*Mean body weight (gms)*	*Species (heaviest to lightest)*	*Sex*	*Mean wing loading index*
Raven	Male	446	Gyrfalcon	Female	1752	Gyrfalcon	Female	32.8
Raven	Female	426	Raven	Male	1383	Gyrfalcon	Male	34.2
Rough-leg	Female	426	Gyrfalcon	Male	1170	Peregrine	Female	35.6
Rough-leg	Male	401	Raven	Female	1085	Peregrine	Male	35.9
Gyrfalcon	Female	396	Rough-leg	Female	1080	Raven	Male	40.1
Gyrfalcon	Male	360	Peregrine	Female	961	Raven	Female	41.6
Peregrine	Female	352	Rough-leg	Male	822	Rough-leg	Female	41.6
Peregrine	Male	308	Peregrine	Male	633	Rough-leg	Male	42.8

*The length of the wing divided by the cube root of body weight.

averaging larger than males. The wings of female Gyrfalcons average about 108 per cent of the average male length; females are about 150 per cent heavier than males, and females have the heavier wing-loading. In Peregrines, female wings average 114 per cent longer than male wings; female body weight runs about 152 per cent heavier. Wing-loading is also heavier in the female. In the Rough-legged Hawk the comparable figures are: 106 per cent for wing length and 131 per cent for body weight. Again females have the heavier wing-loading.

These differences in body size, wing length and also shape, and wing-loading may have important bearings on (a) the kinds of prey that these species can successfully capture, including such variables as size and whether flying or terrestrial, as well as (b) the actual tactics of pursuit and capture employed. The fact that there is a progression of average values for such mensural characters among these four species, as well as between the sexes of each species, suggests behavioral and ecological differences that may indicate different uses of the food resources on a common hunting ground.

Breeding Biology

Basic Data

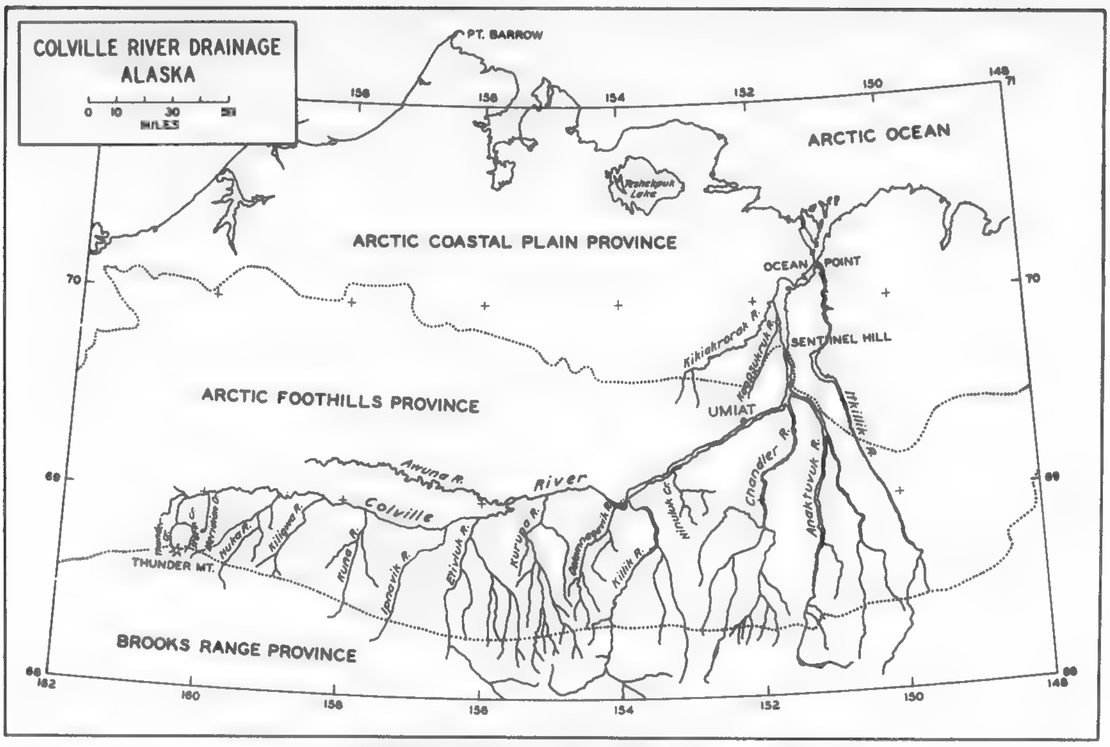
Our presentation is based on data taken from the nestings of 30 pairs of Gyrfalcons, 92 pairs of Peregrines, 208 pairs of Rough-legged Hawks, and 18 pairs of Ravens in the years 1967, 1968, and 1969. We have had combined experience with more than 60 Gyrfalcon, 215 Peregrine, 480 Rough-legged Hawk, and 37 Raven nestings on the Colville River since Cade first traveled the river in 1952; and we have based many of our conclusions on this historical total and not just on the information of the past three years. Interested readers can consult Kessel and Cade (1958), Cade (1960), and White (1969) for detailed information about the years before 1967.

Physical and Biotic Factors Influencing Breeding Distribution

The cliff or bluff is the most important physical feature around which the lives of the four species center during the breeding season. In much of arctic Alaska and especially along tundra rivers such as the Colville, in the foothills section of the Arctic Slope, the cliff nesting habitat forms a conspicuous component of the landscape. Cliffs in arctic Alaska fall into three general categories: River bluffs, isolated upland outcrops, and continuous escarpments in the lower elevations of the Brooks Range. Peregrines, Gyrfalcons, Rough-legs, and Ravens use the first category extensively. Gyrfalcons and Ravens also use the isolated upland cliffs; Peregrines and Rough-legs, which apparently do not, tend to be restricted to river courses. Irving (1960) did not find Peregrines or Rough-legs on the cliffs in the lower elevations of the Brooks Range although Ravens and Gyrfalcons are common there. Apparently the river bluffs in the foothills are the main habitat where all four species nest together.

The distribution of the populations of our four nesting raptors is closely associated with the occurrence of cliffs and bluffs. Bluffs become lower and finally give out completely proceeding north from the foothills into the coastal plain of the Arctic Slope. In this area, the absence of cliffs of significant height probably limits the northern extent of nesting falcons, hawks, and Ravens.

We must study the cliffs from several points of view in order to evaluate their significance as limiting factors. In raptors that require some special part of the cliff for placement of the nest, such as an overhang, there can rarely be



Colville River drainage, Arctic Slope, northern Alaska.

Figure 1. Map of the Colville River drainage and associated portions of the Arctic Slope, northern Alaska. From Kessel and Cade (1958).

a substitute for a cliff (e.g., Gyrfalcons and Ravens in general; see beyond). Rough-legged Hawks, on the other hand, demonstrate considerable flexibility and sometimes build nests on what is essentially the slope of a hill. They also use trees in some parts of their range. Peregrines, it is said, require a given substratum, furnished by the cliff, in which scrapes can be made (see Cade, 1960:164, for discussion), but in our experience this is not the case. Peregrines often simply lay their eggs on a mat of grass. It would seem that Peregrines and Rough-legs could easily move into and exploit ground-nesting situations, and since they have often done so in other parts of their breeding ranges, we wonder why they remain so fixed on cliffs in northern Alaska.

To the south, the rising elevations of the Brooks Range form the boundary of the Arctic Slope. Altitude itself appears to limit at least one of the raptors, the Peregrine. We know of no Peregrines nesting above about 2,200 feet elevation in arctic Alaska. Gyrfalcons, Rough-legs, and to some extent Ravens, reach higher elevations. On the Arctic Slope, at least, it might well be that Peregrines just do not have time to raise young to fledging age at these higher elevations, as in the case of high latitudes. Perhaps the Ravens and Gyrfalcons breed successfully in these higher elevations because (1) they are year-round residents and start nesting earlier, thereby having young near the age of independence when summer climatic conditions are still moderate, or (2) the Gyrfalcon's principal food, ptarmigan, is common in these higher elevations, and the Raven is able to scavenge sufficient food to reproduce. It is interesting to note that they also nest at higher latitudes than the Peregrine.

In the Canadian Arctic Islands and in some other arctic localities, raptors and Ravens breed north to about 75–80° N Lat. At these northern localities the availability of food may be an important factor. For example, Richard Fyfe (pers. commun.) suggested that lack of food may limit, to a degree, either the density or distribution of Peregrines in some parts of the Canadian Arctic.

Further, sheer lack of available time favorable enough to produce young successfully to fledging age, coupled with food scarcity, may limit northern distribution. As Alaska lies below 72° N Lat. it is doubtful that such a combination of physical and biotic factors, linked to high latitude influences on seasonal productivity, would limit northern distribution in Alaska. Should the Alaskan Peregrines, for example, adapt to open ground nesting, as the species has in the bogs of Finland and in parts of the Siberian tundra, then one of the physical factors limiting their distribution — the cliffs — would be surmounted and the vast northern regions of coastal arctic Alaska, where there is also probably sufficient food, would be available for nesting.

On the Arctic Slope, rivers are potent modifiers of both the physical and biotic environments of raptors. Not only do rivers create many nesting cliffs by eroding away hillsides, but also they maintain the riparian habitat essential to some prey species that raptors exploit heavily. The riparian habitat may have a different value to each raptor species, depending on whether it is a closed, dense growth or a more open, scattered scrub. Thrushes and some finches, important as food for Peregrines, prefer the former; some microtines such as *Microtus miurus,* taken by Rough-legs, tend to occupy the latter and, as a result, are more exposed and available. Riparian situations probably are of less importance to Gyrfalcons.

Figure 2. A riparian, wilderness scene along the upper Colville River at the mouth of the Oolamnagavik, viewed from the top of a rocky cliff about 300 feet above the river. 8 July 1967. Northward, the closest permanent human habitation lies 130 miles away on the Meade River; to the east, 60 miles away at Umiat; to the south, 85 miles away at Anaktuvuk Pass; and to the west, about 260 miles away at Point Lay. Within these distances a magnificent stretch of the untouched Arctic waits to be declared a National Wilderness Preserve.

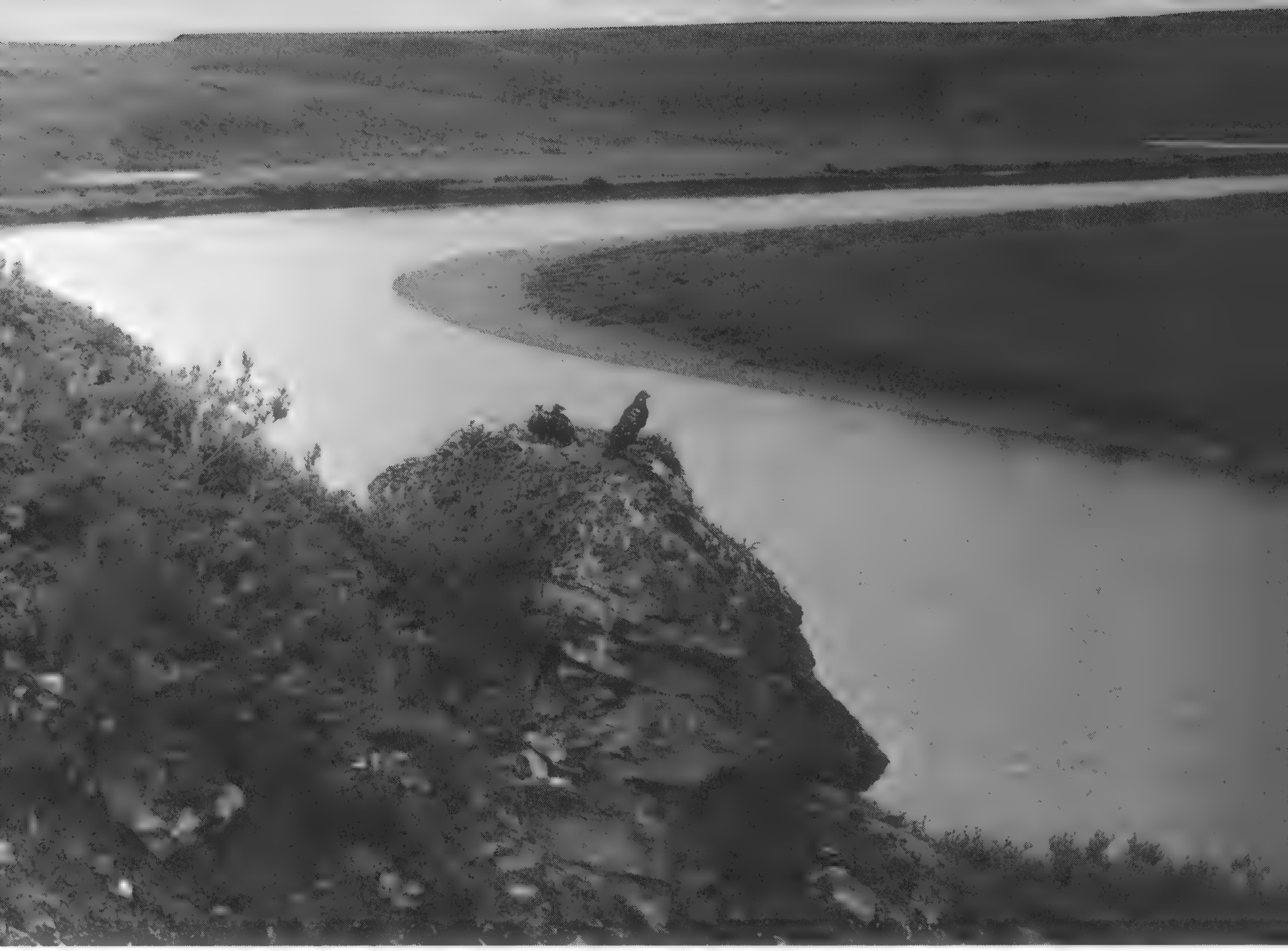


Figure 3. Rough-legged Hawk's nest on top of a rocky projection on a steep hillside. Typical habitat along the upper river. 8 July 1969.

Associated with rivers are gravel bars resulting from the hydrodynamics of the water. Bars may afford several indirect advantages related to raptor distribution. Those that slope gently into the river facilitate bathing, and Peregrines, at least, bathe frequently. Bars are useful for sitting. Young Gyrfalcons, during the fledgling period, characteristically sit on bars. This may be just coincidence because there generally are gravel bars in front of nesting cliffs, or it may be an advantage. Young sitting on gravel bars have a more unobstructed view of terrestrial predators, and the adults can find and feed them more readily on gravel bars than on brush-covered hillsides.

Geography and Geomorphological Structure of the Nesting Habitat

From the mouth of the Etivluk River to Ocean Point, the Colville River flows over a meandering course of about 183 miles (Figure 1), as measured on United States Geological Survey topographic maps with a scale of 1:250,000. Measured as straight lines between the following points, from the mouth of Etivluk River to the mouth of Awuna River to Kakvuiyat Bend to the mouth of Oolamnagavik River to Umiat Mountain to Ocean Point, the distance is 153 miles. Along these stretches of river there are 80 more or less distinct cliffs and bluffs that we judge suitable as nesting habitat for one or more of the four cliff-nesting species.

These cliffs range in length from about one tenth of a mile, or less, to more than four miles; and they are separated from each other by as little as a tenth of a mile, even less in several cases, to as much as 10 and 11 miles in two cases. The average length of cliff is about 0.9 mile, and the average distance apart is about 1.7 miles. The total miles of cliff above Umiat to the Etivluk River are about 34.4; below Umiat to Ocean Point, about 39.0, making a total of 73.4 miles. The heights of these cliffs range from a little less than 50 feet, as is the case of some of the earth formations on the lower river, to about 500 feet at Umiat Mountain (Figures 2–8).

From the Etivluk River to Ishukpak Bluff on the lower river, the cliffs consist mainly of outcroppings of the Nanushuk and Colville Groups, intertongued deposits of marine and non-marine sediments, consisting of sandstone and clay shale with local deposits of coal, bentonite, and tuff. All these formations are from the Lower and Upper Cretaceous (Payne, *et al.,* 1951). North of Ishukpak Bluff, the Colville flows through the coastal plain, an exposed portion of the Continental Shelf. The major geologic formation of this region is the unconsolidated marine and non-marine gravel, sand, silt, and clay of the Gubik Formation of the Pleistocene. High banks and earth bluffs of this formation occur all the way to Ocean Point, giving one the impression of a solid wall of cliff on the west side of the river (Figure 6).

On the lower section of the river the overlying Gubic formation is an important feature in creating "sites" for nests. The Gubic erodes away at a greater rate than the underlying formations. Thus, an average cliff, in profile from the brink, has a sloping face of Gubic terminating in a "nose" or "point" at the junction of the base of the Gubic and the beginning of the underlying clays and shales that normally form a nearly vertical face (Figure 8). These "noses" or "points" provide more or less stable platforms on which a Rough-legged Hawk may build a nest or points where grasses grow, offering "platforms" for the placement of Peregrine scrapes. The juncture of Gubic and

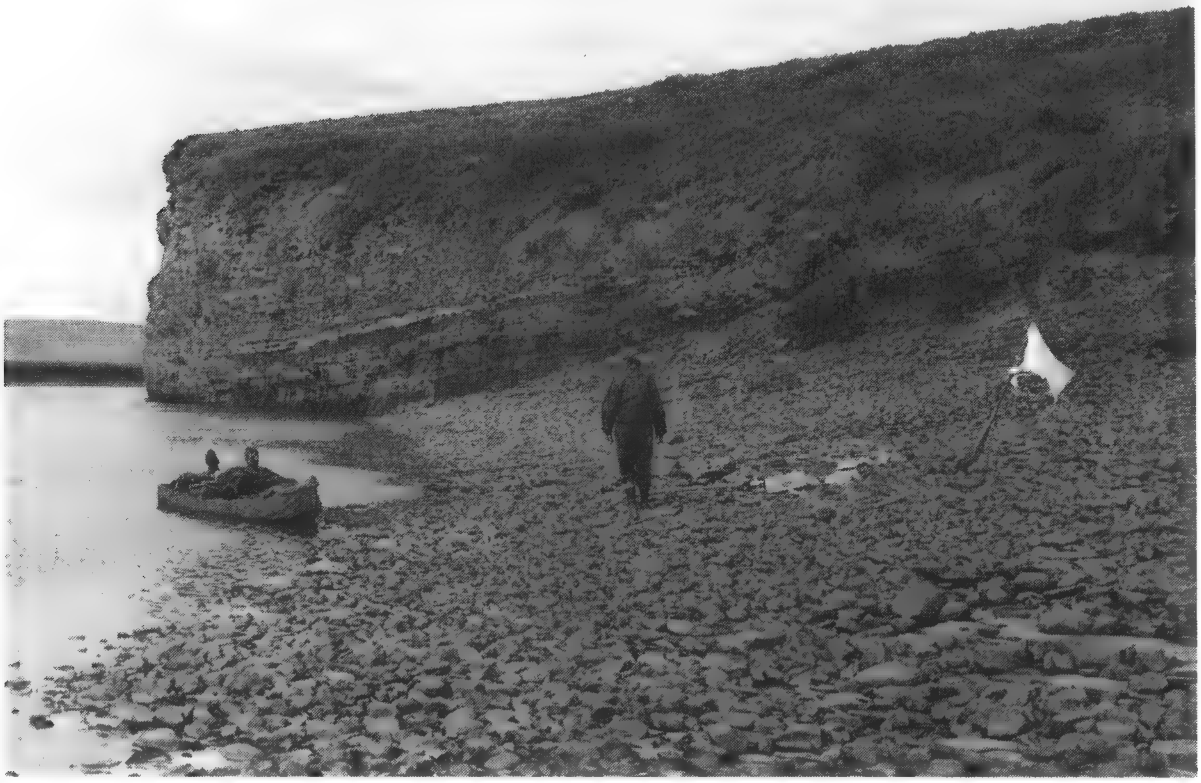


Figure 4. Profile of a shale cliff on the upper river. This formation is typical of many cliffs between the Etivluk and Killik Rivers. Peregrines and Rough-legged Hawks both nest here. This cliff is about 100 feet high and is slightly undercut by the river. 26 June 1967.

TABLE 2

Colville River Cliffs and Their Occupancy by Rough-legged Hawks (RL), Peregrine Falcons (P), Gyrfalcons (G), and Common Ravens (R)*

*Cliff number***	*Occupancy in 1969*	*Occupancy in 1968*	*Occupancy in 1967*	*Combined occupancy (1952–1959, 1964) where known*	*Length in miles*	*Miles to next cliff*	*Number of old stick nests (1967)*
1	P RL	P RL	P RL	P RL	0.5	5.0	2
4	RL			RL R	0.1	3.5	1
5	P	RL	R	P RL R	0.25	1.0	1
6	RL	RL R	P$_1$ RL	G P RL	0.5	1.2	0
7	P RL	P RL	P RL	G P RL	0.2	0.2	2
8	RL	RL	RL	RL	0.5	1.5	2
9	P 3RL	P 3RL	P 3RL	P RL	1.0	1.0	0
9a	RL	RL (site on hillside, no cliff)			—	—	—
10	RL	RL	RL	RL	1.0	1.0	1
11	RL	RL	RL	RL	0.75	2.25	2
12	P RL	P RL	P RL	P RL	0.3	0.5	0
13	RL R	RL	R	G RL	0.25	0.6	6
14	P RL$_1$	P	P RL	P RL	0.5	1.5	1
15	RL$_1$	RL$_1$ R	RL$_1$		1.25	3.5	0
16	RL		RL$_1$		0.5	1.5	0
17	RL$_1$			RL	1.0	2.5	1
18					0.5	1.5	0
19					0.5	0.1	0
20	G 2RL	G RL	G RL	G RL	2.0	0.25	1
21	RL	R	RL$_1$ R?		1.0	1.5	0
22					0.5	1.0	0
23					0.5	2.0	0
24		RL$_1$ R			0.75	3.0	0
25					1.0	3.0	0
26	RL	RL	RL		0.5	3.0	0
27	RL	RL	RL	RL	1.0	1.2	1

TABLE 2 (Continued)

*Cliff number***	*Occupancy in 1969*	*Occupancy in 1968*	*Occupancy in 1967*	*Combined occupancy (1952–1959, 1964) where known*	*Length in miles*	*Miles to next cliff*	*Number of old stick nests (1967)*
28	P RL R	G P RL	G P RL	G P RL	0.75	1.25	0
29	RL	RL	RL		0.25	1.0	0
30	RL			RL	0.5	1.25	1
31					0.25	1.25	0
32	RL	RL	RL		0.1	0.75	0
33				G	0.5	1.0	0
34	P RL	P RL	P RL	P RL	0.5	1.5	1
35			R_1		0.4	0.25	0
36	RL	RL		RL	0.25	0.5	3
37			RL_1		0.1	1.25	0
38	not checked	RL	RL	RL	0.25	1.0	1
39	RL R	RL	P_1 RL	P RL	0.75	1.0	1
40	RL		RL	P RL	0.6	0.75	3
41	G P 3RL	G P $2RL_1$ R	G P 2RL	G P RL R	1.0	1.0	0
42					0.25	0.1	0
43	RL	RL	RL	RL	0.3	0.1	1
44	P	G P RL	P RL	G P RL R	0.5	3.5	1
45	G P RL	G RL R	G RL	G P RL R	1.0	4.5	1
46	RL_1	P RL	P RL	G RL R	1.0	10.0	0
47	P RL	G P	G P_1 RL	G P RL R	0.5	1.5	2
48	G P RL	G P	G P RL	G P RL	1.5	1.2	0
49		RL	RL	P	0.25	8.5	0
50	RL	RL	RL	G P RL	0.25	2.0	4
51	RL			P RL	0.3	4.0	0
52	G P 2RL	P RL R	G P 2RL	P RL	1.25	5.0	0
53	G P RL	G P	G P RL	G P RL	0.75	3.5	0
54	G 2RL R	G P RL	G P 2RL R	G P RL R	1.0	1.0	3
55	P RL		RL	P RL	1.0	4.0	1
56	RL_1			RL	0.2	2.5	0

TABLE 2 (Continued)

*Cliff number***	*Occupancy in 1969*	*Occupancy in 1968*	*Occupancy in 1967*	*Combined occupancy (1952–1959, 1964) where known*	*Length in miles*	*Miles to next cliff*	*Number of old stick nests (1967)*
57	G P 3RL	P RL R	P 3RL R	P RL R	1.0	2.5	0
58	P 3RL	G P 2RL R	P 2RL	P RL	2.0	0.25	0
59	G 3P $7RL_1$	G 2P 3RL	G 2P 6RL	G P RL	4.5	2.0	0
60	P 2RL	P RL	P RL	P RL	2.0	0.2	2
61	P 3RL	2P 2RL	G RL	P RL	2.0	0.1	0
62					0.2	0.1	0
63	3P 6RL	3P 4RL	3P 5RL	P RL	1.75	0.1	0
64	P 4RL	3RL	P RL_2	RL	4.0	1.0	1
65	P RL_1	P R	P_1	P	0.75	0.1	0
66	RL		R_1		0.4	0.1	0
67	P 4RL		RL		1.5	0.1	0
68	2P $4RL_1$	2P 3RL	2P RL	P RL	4.0	0.1	2
69	P 2RL	P RL	RL		1.0	0.1	0
70	RL	RL	RL		1.2	0.1	0
71					0.4	0.2	0
72	RL		P RL	P RL	0.5	11.0	0
73	RL	RL	RL	P RL	1.5	0.5	0
74		RL		P	0.5	1.0	0
75	P 2RL	P RL	P RL	P RL	1.5	0.2	0
76	RL				1.0	0.2	0
77	2RL		P_1	P	0.3	0.1	0
78	$1RL_1$		RL?		0.5	0.1	0
79	RL_1	2P 2RL	P 2RL	P RL	5.0	0.1	0
80			P	P	1.75	0.1	0
81					0.6	—	0
				Mean	0.92	1.7	

*Number preceding letter = number of pairs; subscript number = single adults.

**Cliffs 2 and 3 are omitted because they are unsuitable as nesting habitat for cliff-nesting birds.

shales varies in distance below the brink of the cliff from perhaps five feet, where the Gubic first appears, to about 30 feet on the downriver stations.

The noses or points created by the morphological feature of Gubic overlying shale provides places for nests far enough below the brink of the cliff to give some protection from terrestrial predators. At the same time, however, any one point or nose may not last out the nesting season because the expansion or shrinking of the substratum in alternating wet and dry spells, or thawing permafrost, results in rapid erosion and sloughing. The faces of Cliffs 69 to 72 (see Table 2) are shale and clay and nearly vertical from brink to base. The lack of secondary noses below the brink may be one of the reasons why we seldom found falcons on these rather "sterile" sections.

One curious fact that emerges from our data is that there are conspicuous gaps in the use of nesting habitat by Peregrines and Rough-legs. The Rough-legs, being the most numerous and much less restricted to specific structures, such as overhangs, for nesting, should use the habitat fully. Yet, large gaps in occupancy of suitable looking cliffs by Rough-legs occur between Cliffs 16 and 20 and between Cliffs 21 and 26. Cade noted similar voids in 1952 and 1959. Raptors have never occupied Cliffs 18, 19, 22, 23, 25, and 31. These gaps are of particular importance in that Rough-legs occupied a bushy hillside at Cliff 9a for two years, and two or more pairs nested on several cliffs above and below the vacant ones. Between Cliffs 57 and 61, about 15 linear miles of river with 11 miles of cliff, there were no less than 18 pairs of hawks in 1967 and 24 pairs in 1969. Because of the sheer numbers of Rough-legs, their nests were frequently close to one of the other species. In 1967, for example, 40 out of 62 nestings were less than half a mile from one of the other species. We also noted conspicuous voids in the use of cliffs by Peregrines and cannot explain why such gaps exist in apparently suitable habitat.

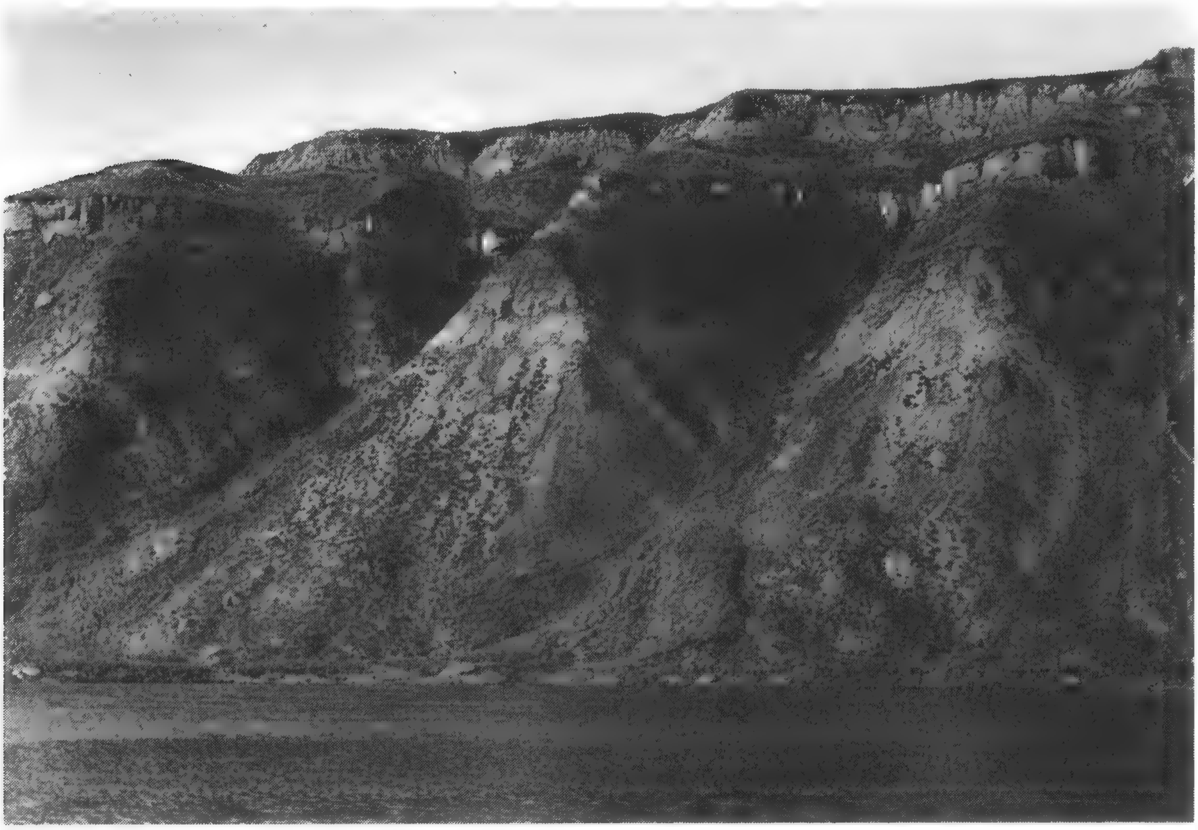


Figure 5. A portion of Shivugak Bluff, which represents some of the highest and most continuous cliff on the lower Colville. The top of the section shown here is more than 400 feet above the river. Peregrines, Gyrfalcons, Rough-legged Hawks, and Ravens have all nested in this area. 28 July 1967.

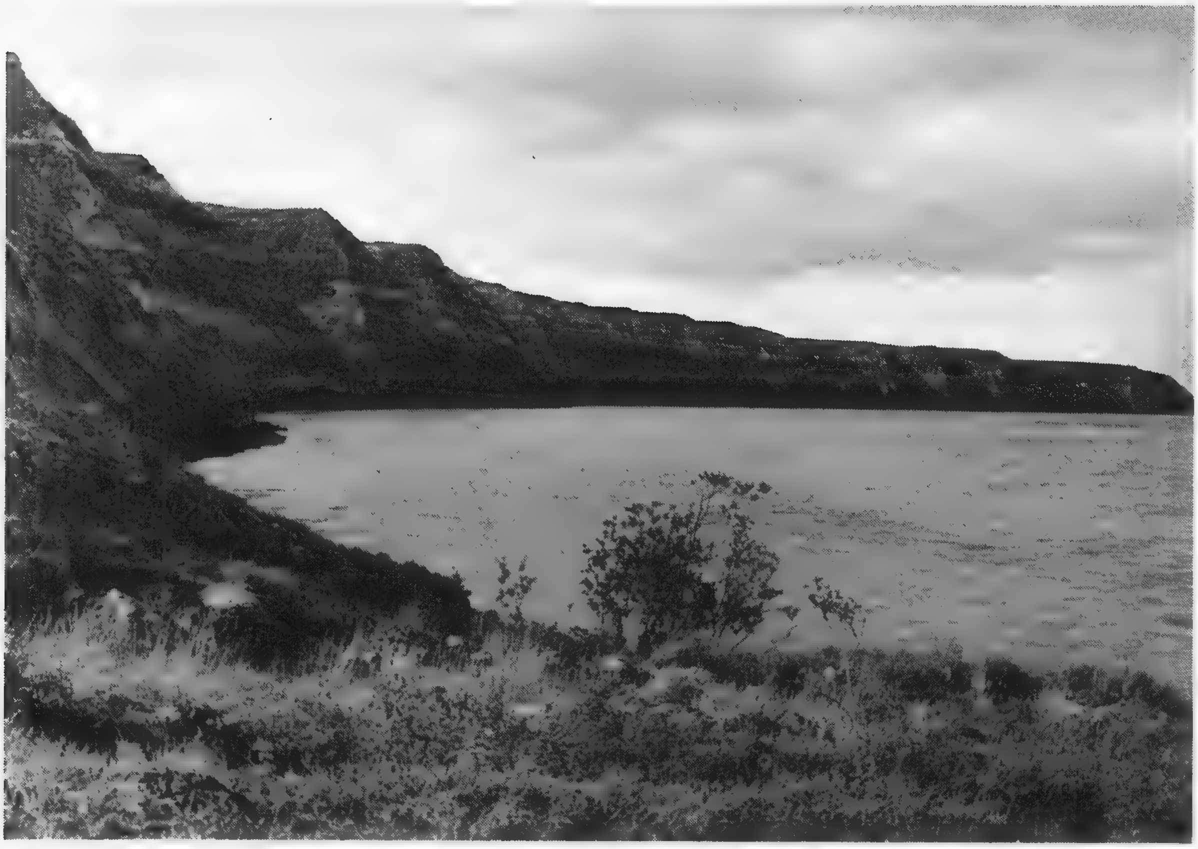


Figure 6. Uluksrak Bluff, showing the continuous nature of the bluffs lining the left limit of the Colville from Umiat to Ocean Point. As many as three pairs of falcons and six pairs of Rough-legs have nested simultaneously on this 1.75 mile stretch. 1 August 1967.

Historical Occupancy of Cliffs and Distribution of Used Cliffs

One of the significant marks of raptor biology is the repeated occupancy of traditional nesting sites whether on cliffs, in trees, bogs, or other habitat. Of the species nesting in cliffs along the Colville, this trait is most striking among the Peregrines and Gyrfalcons (see discussion in Cade, 1960; White, 1968b). Ravens in the boreal and deciduous forests of eastern United States apparently use the same nesting region for many successive years. Ravens in arid western deserts traditionally use the same cliff, at least, for placing their nests. Wolfe (1929), for example, collected Raven eggs from two localities in Skull Valley, Utah, in the late 1920's, and Ravens were still nesting on those same sites in 1950, 1961, and 1964. Ratcliffe (1962) documented the stability and traditional use of nesting sites by Ravens in England.

Table 2 contains a summary of the historical occupancy of 80 cliff units on the Colville River for the years 1952, 1956, 1957, 1958, 1959, 1964 (part of the river), 1967, 1968, and 1969. We omitted Cliffs 2 and 3 because we judged them unsuitable for nesting and recently added Cliff 9a. Of these 80 cliffs, 71 (89 per cent) have been used by one or more hawks, falcons, or Ravens; with 21 (26 per cent) used by Gyrfalcons, 40 (50 per cent) by Peregrines, 69 (86 per cent) by Rough-legged Hawks, and 20 (25 per cent) by Ravens.

From our knowledge of the habitat requirements of the species, we feel safe in saying that the nine years of data from our studies represent the conditions that existed in years when no studies were made. For example, Peregrines probably never use more than 50 per cent of the available habitat. We have compared the number of cliffs used each year with the total number known to

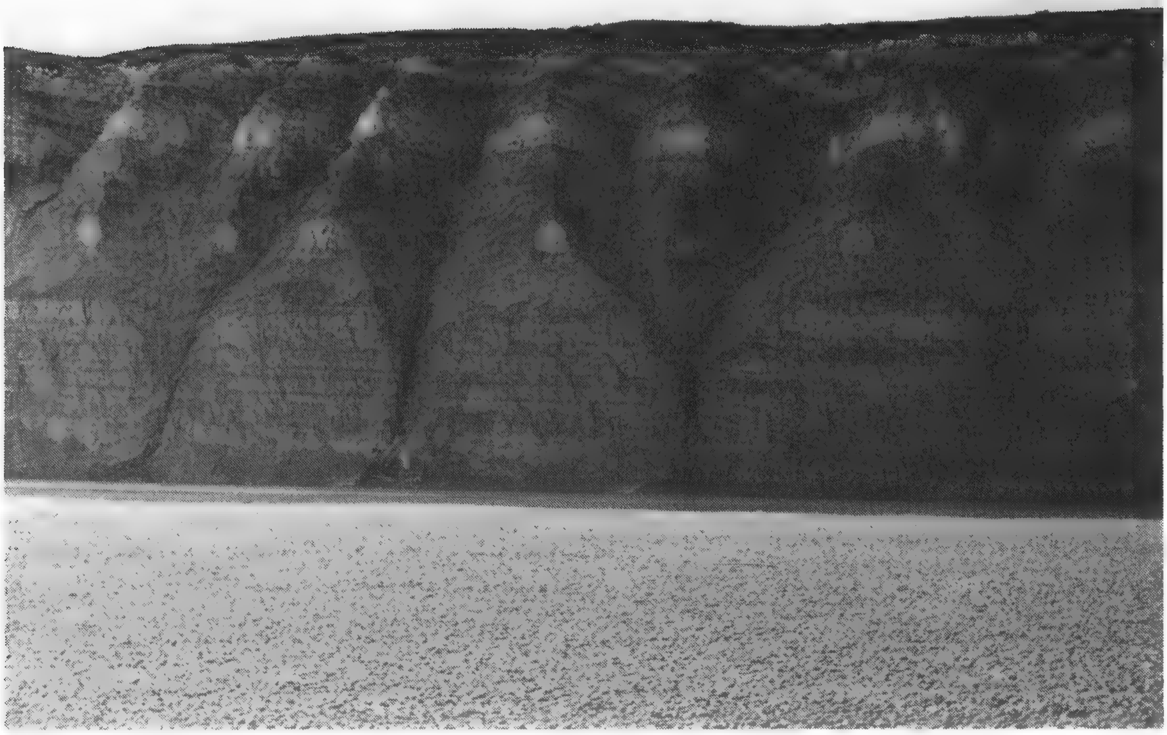


Figure 7. A frontal view of typical bluff on the lower river with "flat iron" faces, nearly perpendicular, forming the lower part of the bluff, with prominent rocky "noses" above, and less precipitous ridges running up to the upper rim or break at the tundra's edge. Here the birds always nest in some position above the flat iron faces. 28 July 1967.

have been used previously (Table 3). The data suggest that these four species find only certain cliffs suitable out of the total number available for nesting, and that they use these same cliffs year after year. Although the entire significance of this behavior is not clear, it does space out the population and may reduce intraspecific competition.

We consider a pair or a single resident individual as one unit. In 1967, one or more Units of Rough-legs, Peregrines, Gyrfalcons, and Ravens occupied 59 cliffs. Seven cliffs had only single individuals. The total of 106 pairs, 117 units, gave an average of one nesting pair per 0.7 mile or cliff and per 1.73 linear miles of river. The closest nestings between adjacent pairs, among all species considered, was 60 yards between a Raven and Gyrfalcon and between a Rough-leg and Gyrfalcon; the greatest distance between adjacent pairs was 13.5 miles. The greater distances are more a function of sections of river without cliffs, with unsuitable cliffs, or with cliffs that look suitable but historically have not been used than they are of a readily observed biological or behavioral factor such as interspecific or intraspecific aggression.

In 1968, one or more units of raptors occupied 51 cliffs with a total of 111 pairs, 114 units, an average of one pair per 0.66 mile of cliff and per 1.65 linear miles of river. The closest nesting between adjacent pairs was very unusual — about 10 yards between a Rough-leg and a Peregrine.

In 1969, raptors occupied 63 cliffs — three with single individuals only — giving a total of 140 pairs, 143 units, with an average of one pair per 0.52 mile of cliff and per 1.31 linear miles of river. The closest nesting was about 50 yards between a Rough-leg and Peregrine. Additional pairs of Rough-legs accounted for most of the increase over the previous year.

There is a decided difference in the density and distribution of species along different sections of the river. For convenience we have divided the river just below Umiat into the upper, Umiat Mountain to Etivulak River, and lower, Umiat Mountain to Ocean Point, sections. The approximately 127 miles upriver contain 55 cliffs but only 35.4 miles of cliff; the 56 or so miles downriver contain 23 cliffs with 38 miles of cliff.

On the upriver section, for all years combined, Gyrfalcons have occupied 18 cliffs (33 per cent of the total), Peregrines 25 (45 per cent), Rough-legs 49 (89 per cent) and Ravens 17 (31 per cent). On the downriver cliffs, Gyrfalcons occupied 3 (13 per cent), Peregrines 15 (65 per cent), Rough-legs 22 (96 per cent), and Ravens 3 (13 per cent). Gyrfalcons and Ravens used a conspicuously higher percentage of cliffs upriver than downriver. We have never found Gyrfalcons nesting downriver from Cliff 61 although we occasionally saw single Gyrfalcons below there. The fact that the Peregrines, which could be competitors for nest sites, are denser downriver than upriver may account for the absence of breeding Gyrfalcons. More likely, however, the difference in falcon density between upriver and downriver results from the structure of the cliffs. There are simply not enough ecological situations — firm rock with overhang — for Raven and Gyrfalcon nests, while the more flexible Peregrines and Rough-legs are able to take advantage of the many cliff brinks and noses for placing their nests.

For the combined years, 46 pairs of Peregrines nested at a density of one pair per 8.3 miles above Umiat Mountain, and 45 pairs nested at one pair per 3.7 miles below Umiat Mountain, with an overall average of 6.03 river miles apart. The closest nestings were about 0.4 mile; the farthest, about 27 miles apart. The minimum distance between pairs of Gyrfalcons was about 2 miles,

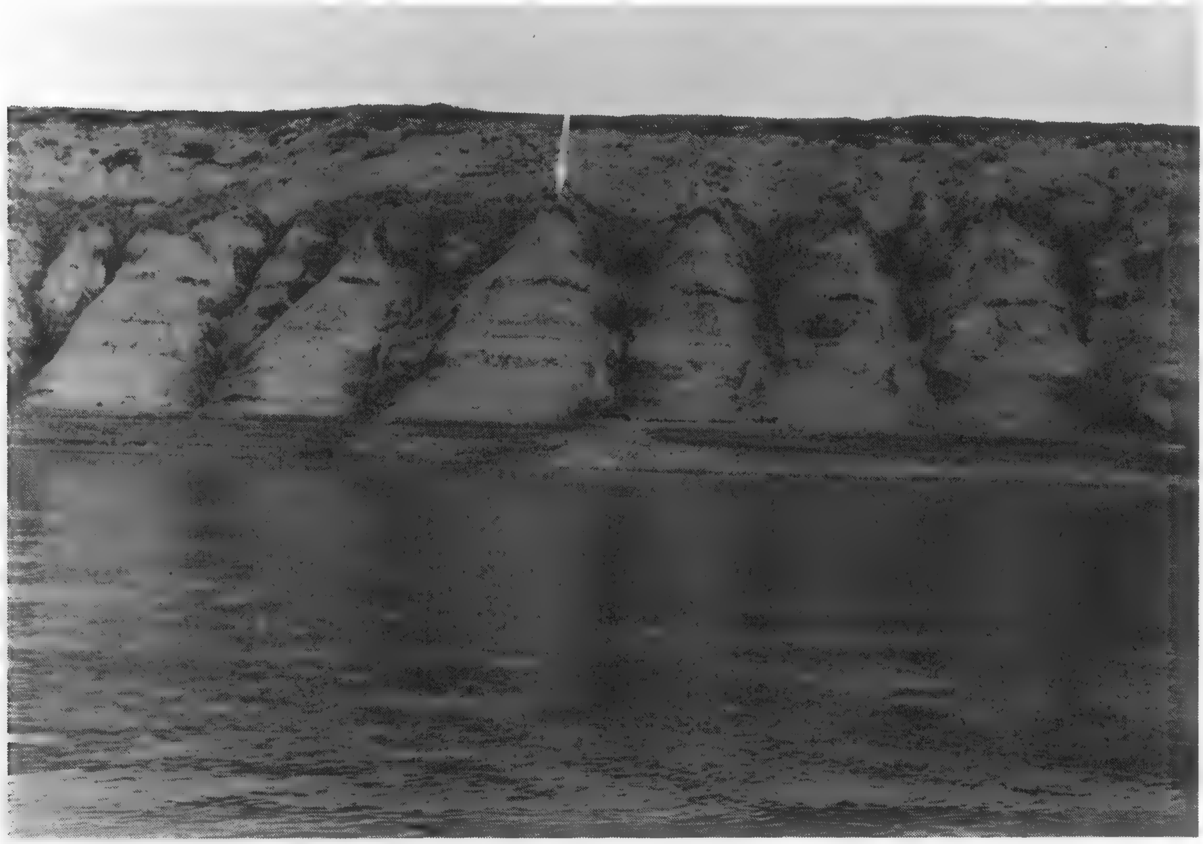


Figure 8. A low bluff on the lower river near Ocean Point, showing the Gubic Formation overlying the more resistant shale and clay. Peregrines and Rough-legged Hawks nest on the noses or apexes (indicated by the white arrow) of the faces, usually in a grassy area. The top of this cliff where the tundra begins is about 50 feet above the river.

TABLE 3

Comparison of Cliffs Used Each Year by Raptors and Ravens with Total Number of Cliffs Known to Have Been Used Previously

Species	*Year*	*Cliffs used*	*Percentage of cliffs used*	*Percentage of cliffs used that were used all 3 years*
Gyrfalcon	1967	11	52	
21 cliffs available	1968	11	52	
	1969	9	43	
	1967–1969			64
Peregrine	1967	30	75	
40 cliffs available	1968	25	63	
	1969	27	68	
	1967–1969			67
Rough-legged Hawk	1967	51	73	
69 cliffs available	1968	46	69	
	1969	61	88	Not determined
Raven	1967	4	20	
20 cliffs available	1968	10	50	
	1969	4	20	0

the maximum, about 24 miles, and the average about 10.9 miles. Rough-legged Hawks nested at a minimum distance of about 0.25 mile, and a maximum of about 13.6 miles, with an average of 2.4 miles. Nesting pairs of Ravens averaged 21.1 miles apart with a minimum distance between them of about 3.5 miles and the maximum distance about 102 miles.

Spatial and Temporal Use and Division of the Nesting Habitat

The four species demonstrate not only considerable overlap in several ecological variables in their breeding biology but also some rather distinctive uses of the habitat. Two other aspects of major importance are the seasonal timing in the use of food and nesting habitat and the actual physical placement of nests on cliffs.

Spacing.—We may make a terse statement about the average nesting situations used, or chosen (?), by the species. Table 4 shows three differences in the way they place their nests on the cliffs. Figure 9 gives a further analysis of the height above the river. Rough-legs, apparently rather versatile in the substratum they choose for a nest and the location on the cliff, completely overlap the other three species in these variables. Rough-legs usually place their nests on ledges, or other suitable platforms, on vertical faces (Figure 10), although even in the region of rocky outcrops, we found some nests on steep talus slopes below the rocky outcrop and others at the break in the slope of a high earth bluff or on top of a rock on a steep hillside (Figures 3 and 11). Below Ishukpak Bluff, where hard rock is generally lacking, the hawks habitually choose a break in slope — a semi-stable point or irregularity of strata, caused by the interface of shale overlain by sand. These nests, predominately on talus slopes, are most subject to destruction by earth and mud slides. Rough-legs nest successfully close to any one of the other species (Table 5), but the nesting of adjacent pairs of Rough-legs is spaced out in a manner similar to the spacing between pairs of Peregrines.

Peregrines also accept a wide variety of sites for nesting (Figures 12–14). Where good, rocky outcrops occur, they perhaps most often choose a ledge or platform, including old stick nests of Rough-legged Hawks, on a vertical face though this is by no means always the case. Even on the upper river where rocky outcrops are most frequent, some Peregrines nest at the brink of a cliff or on a nose at the break in slope of a steep earth bluff, or sometimes at the base of a rocky face above a talus slope leading down to the river. On the lower river they place their nests most often at the apex of "flatiron" formations or on noses at prominent breaks in the slope of earth bluffs. In the past, up to 19 per cent of the falcon aeries were in old stick nests of the Rough-legged Hawk (Cade, 1960). Table 2 shows that in 1967, when 49 old nests were available, only one pair of Peregrines used a stick nest. The 57 Colville Peregrine aeries, reported by Cade (1960) for the years 1952–1959, show nearly the same variation in placement on the cliff as our 1967–1969 sample.

Gyrfalcons have stricter requirements for nesting sites than either Peregrines or Rough-legged Hawks (see Cade, 1960). It is therefore more difficult to determine how much suitable nesting habitat is available for them. Basically, because they breed early in the season, they require a ledge or platform protected from snow accumulation by an overhanging projection of rock. To illustrate this point more graphically we have tabulated our data on description of Gyrfalcon aerie sites (Table 6) in order to compare them with all the 1967 Peregrine sites (Table 7), which also are typical of those in 1968 and 1969 (Figures 15–20).

Unless Gyrfalcons have bred at a particular cliff, it is often difficult to decide whether a cliff is suitable or not. Another complicating factor is that a cliff may become suitable for Gyrfalcons after it has been used by Rough-legs or by Ravens, for the Gyrfalcons depend very much on old stick nests for their aeries; or a cliff may become unsuitable when a stick nest is destroyed. There are now 21 cliffs along the Colville where we know Gyrfalcons have nested at one time or another between 1952 and 1969.

The Raven, like the Gyrfalcon, is an early breeder and has almost exactly the same requirements for nesting sites (Figures 19 and 20). In fact, the Gyrfalcon more frequently uses the old stick nest of the Raven for its own aerie than any other type of site. The Raven must, therefore, be counted as an important factor favorably modifying the environment for the Gyrfalcon. We have no recorded observations to prove that Gyrfalcons build their own stick nests as is sometimes stated; the fact that both species nest at the exact sites in

TABLE 4
Placement of Raptor and Raven Nests on Cliffs in 1967, 1968, and 1969

	Vertical measurements in feet			
	Gyrfalcon	*Peregrine*	*Rough-leg*	*Raven*
Number of nests with data	22	80	181	10
Distance above river				
Mean	95.4	116	111	63.5
Range	20–300	30–400	10–400	25–250
Per cent below mean	74	65	69	80
Distance below cliff brink				
Mean	32	33	39	17.8
Range	5–200	0–150	0–200	5–100
Per cent below mean	70	70	70	80
Distance above cliff base				
Mean	27	54	56	17.3
Range	6–70	0–300	0–300	10–25
Per cent below mean	59	69	67	66

different years argues in favor of the Raven as the original constructor of all these nests. The Gyrfalcon and Raven, then, are the only two of the four species that frequently use the exact same portion of the cliff.

The use by each species, except for the Gyrfalcons and Ravens, of a slightly different portion of the cliff (Table 4), may reduce competition for nesting sites. The nests of Gyrfalcons and Ravens are, on the average, on lower cliffs relative to the river and closer to the base of the cliff. Their similar requirements for nesting under an overhang on a rocky face may result in contests between pairs of Gyrfalcons and Ravens for especially suitable sites. See discussion beyond.

It would be instructive to know whether the differences, shown in Figure 9 and Table 4, in nest heights above the river are statistically significant. One could then place some reliability on statements about trends to avoid competition by locating the nests in different parts of cliffs. The nature of our data, however, is such that they are difficult to treat statistically for the following reasons. To obtain large samples we must lump the various years, thereby masking the variation in any one year. It is most critical to know what is taking place on a given cliff where any combination of the four species are together, but such a sample size would be very small when considering Gyrfalcons or Ravens. Further, nest site tenacity and traditional use obscure any evidence of the interaction that may have occurred early in each season or early in a historical sense. Thus statistical treatment is of limited value, but a test (the Mann-Whitney U test), in which few assumptions must be made, indicates a suggestion of differences. In considering the height of the nest above the river, two different species may have significant differences — i.e., a comparison of Gyrfalcon versus Peregrine yields a Z value of 1.94 where P = 0.052; and Gyrfalcons versus Rough-legs yields a Z value of 3.21 where P = 0.001. These tests indicate that Gyrfalcons tend to use a different section of cliff than either Peregrines or Rough-legs.

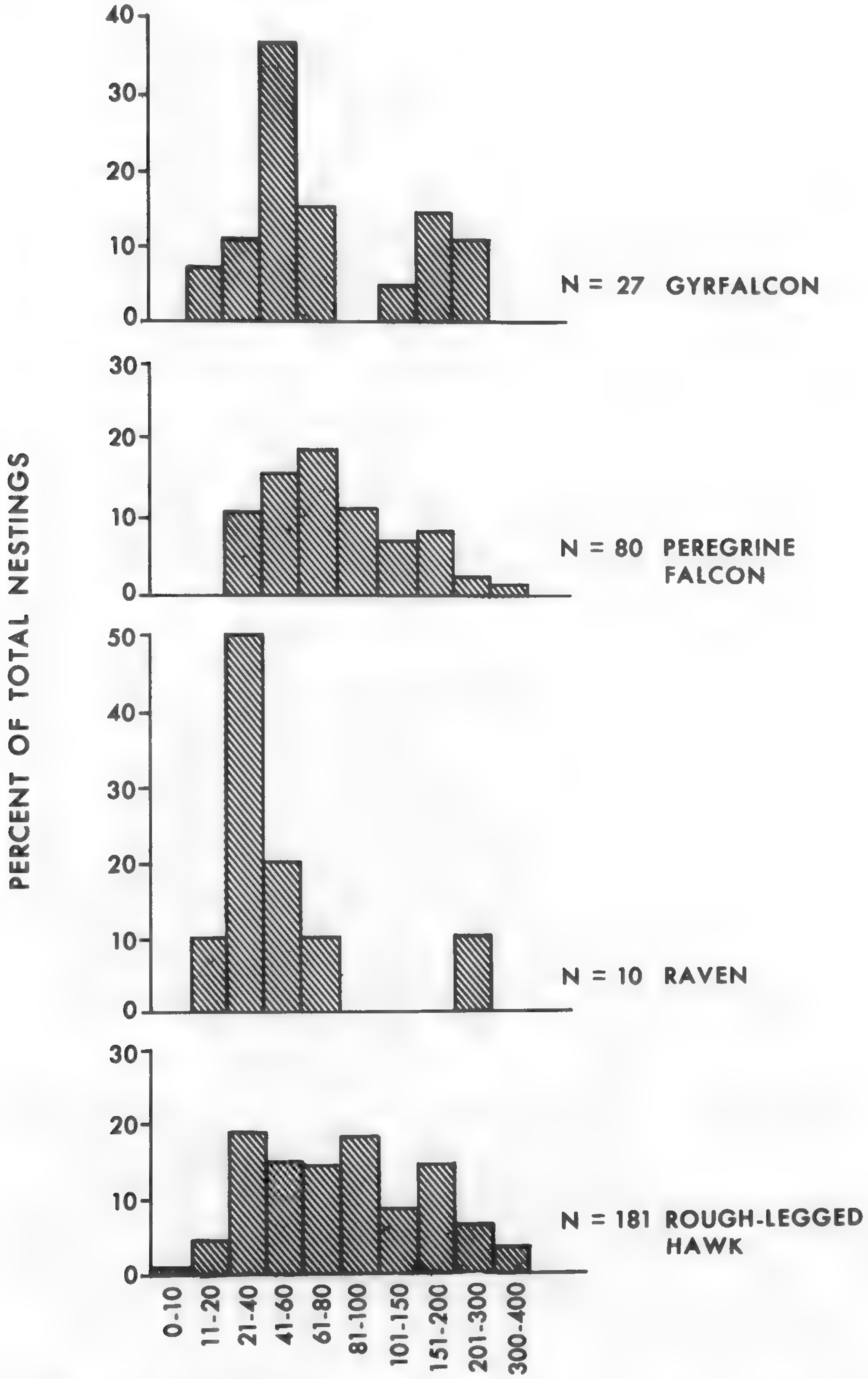


Figure 9. Bar graph showing the heights of nest placement in vertical feet above the river for Gyrfalcons, Peregrines, Rough-legged Hawks, and Ravens. N = the number of nests for each species.

Timing.—Gyrfalcons and Ravens, essentially residents on the Arctic Slope, are present at their nesting cliffs before the arrival of the bulk of the migrant Peregrines and Rough-legged Hawks. Perhaps many individual Gyrfalcons and Ravens may remain near their nesting sites the year round. This one single phenomenon affects, to a degree, the numbers of nesting choices open to Peregrines and Rough-legs upon their arrival. Ravens are on eggs, probably by mid-April, at the time Peregrines arrive in the Arctic. Possibly, Peregrines can dislodge Ravens, in physical contest, from prime nesting sites should Peregrines want to occupy them, but we have no data on this point. Gyrfalcons are likewise on eggs about mid-April when Peregrines arrive. Cade (1960) indicated that Peregrines are physically unable to dislodge Gyrfalcons from nesting sites, but their attempts to do so may constitute a real point in competition between these two congeners.

One question that we still need to answer is that of competition for nesting sites between the early breeding Ravens and Gyrfalcons. In 1967 and 1969 at Cliff 13 we found Ravens nesting on the same ledge where Gyrfalcons used stick nests in 1952 and 1959 (Figure 19). In 1969, Ravens used the exact nest that Gyrfalcons had used on Cliff 28 in 1967 and 1968 (Figure 16). We found a similar situation on the Oolamnagavik River in previous years and have reports of it from other arctic locales as well (see Cade, 1960). Gyrfalcons evidently sometimes take over occupied Ravens' nests and even kill the adults. The final answer to the question of Raven-Gyrfalcon interaction must await observation by investigators working on the Colville as early as March and April when Ravens and Gyrfalcons are setting up territories.

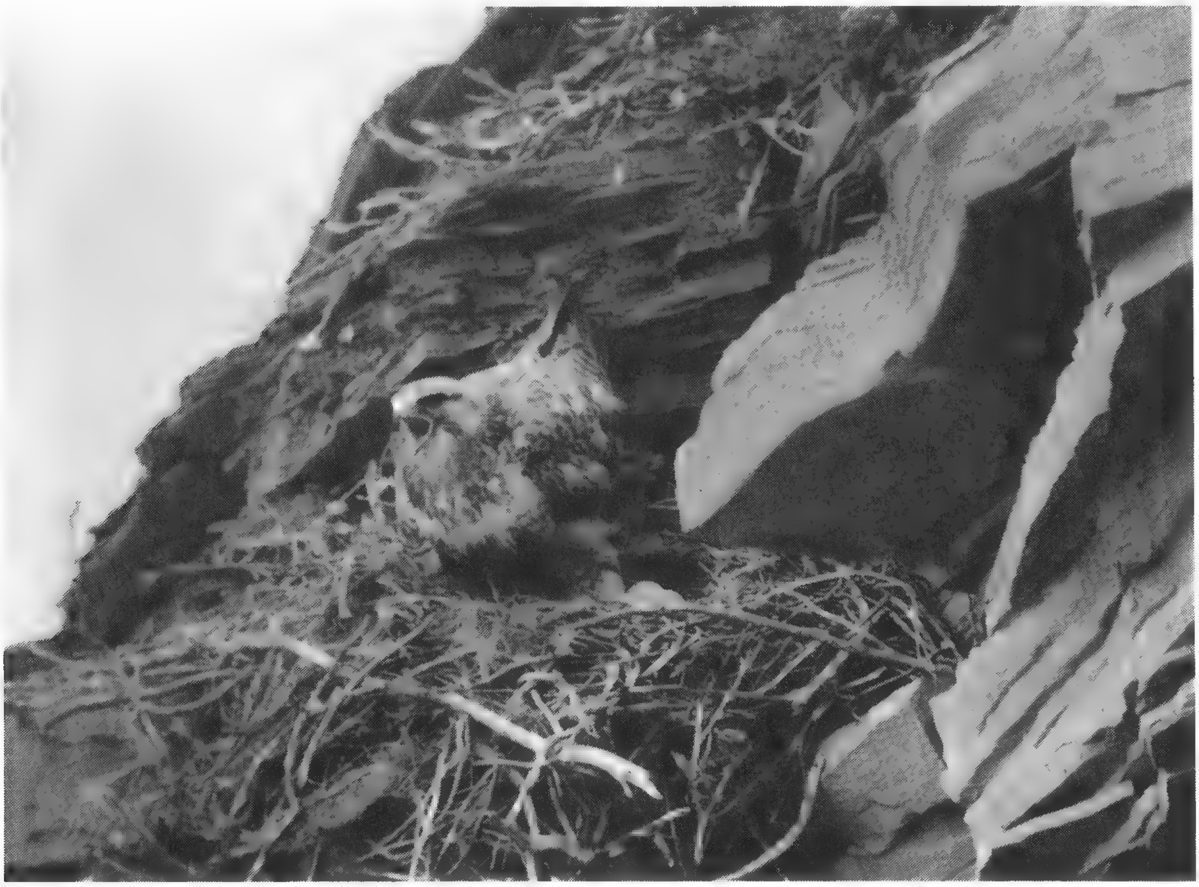


Figure 10. Adult male Rough-legged Hawk covering a nest situated on a sandstone outcrop near the mouth of the Etivluk River. 18 June 1967. From a kodachrome by W. R. Spofford.

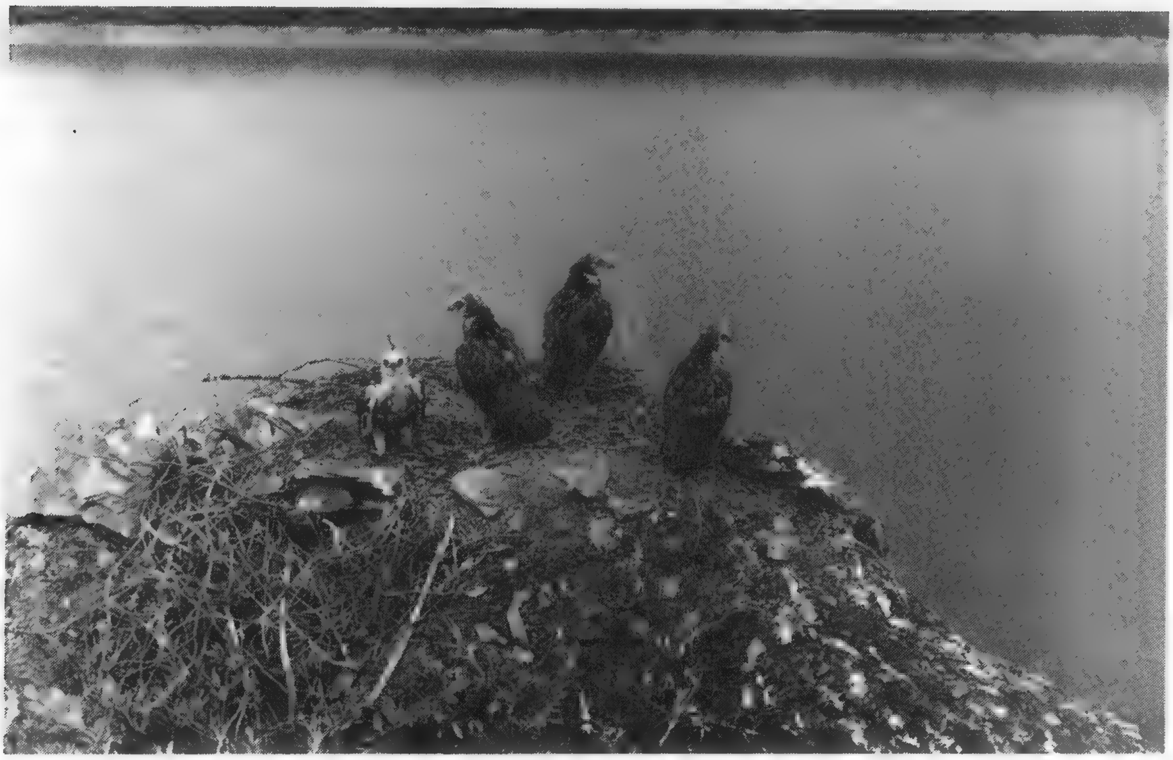


Figure 11. Brood of nearly fledged young Rough-legs in a nest on top of a rock. Same nest as depicted in Figure 3. 24 July 1969.

It certainly appears that Peregrines can dislodge Rough-legs from nesting sites even though both arrive in the Arctic at about the same time. In 1968, a Peregrine on Cliff 47 incubated her two eggs in a Rough-leg nest that contained two Rough-leg eggs. Rough-legged Hawks were not nesting elsewhere on the cliff although one adult was seen soaring just upriver. Possibly the Peregrines, in order to use this site, dislodged the Rough-legged Hawks that had already started egg-laying. In 1969, Rough-legs nested once again in that site, and Peregrines nested about 100 yards away on the cliff brink.

Timing is readily reflected in food habits. Gyrfalcons rely mainly on ptarmigan which are available throughout the winter and at the onset of courtship and egg-laying, before the arrival of migrant birds. This factor may be of special importance in allowing Gyrfalcons to breed early. Ravens may also breed earlier because they can scavenge and augment their diets with the kill remains of prey from Gyrfalcons as well as from wolves and other carnivores.

The importance of food availability to the timing of the onset of nesting is also reflected at later stages of the breeding cycle. Gyrfalcons begin to fledge young just as ptarmigan hatch, and the young ptarmigan provide a greatly expanded resource for fledgling Gyrfalcons and perhaps actually enhance their survival rate at this critical period. Peregrine eggs, on the other hand, hatch simultaneously with those of the passerines and shorebirds. Since the smaller male Peregrine provides food for the nestlings when they too are small, the fledgling passerines and shorebirds may be the best food resource in the size range that he is able to catch.

Food Habits

The primary food relationships of Gyrfalcons on the Arctic Slope are with resident species of mammals and birds, particularly the ptarmigan (Table 8). Peregrines, dramatically more catholic in their choice of prey, rely mainly on a wide variety of migratory birds (Table 9). They may also concentrate on certain species that are very abundant or concentrated locally in any one year. The main food relationships of the Rough-legged Hawk are with microtine rodents (Table 10). We have not tabulated the food of Ravens because we have too few data from their nesting sites. Several hundred pellets, collected from a winter roost at Umiat, are not yet completely analyzed; food remains from pellets, gathered below nests, contained remains of ptarmigan, fish, microtine rodents, and passerine birds. The Raven's diet covers a broad spectrum of foods and spans the entire range of foods used by the other three species. It is not clear whether the Ravens catch most of their prey in active pursuit or pick it up mainly as carrion. Doubtless they use both methods. The frequency with which ptarmigan and microtine remains occur in their pellets suggests that Ravens prey actively upon these species. Weir (1967), on the other hand, watched Ravens eating kill remains at a Gyrfalcon perch in Iceland, a habit that could account for the many ptarmigan and bird remains in Raven pellets on the Arctic Slope. Possibly, Ravens place their nests on the

TABLE 5
Proximity to Other Nests in 1967, 1968, and 1969

	Gyrfalcon	*Peregrine*	*Rough-leg*	*Raven*
Gyrfalcon				
Average distance to nearest nest*	0	370	298	35
Nearest recorded nest*	0	40	60	20
Number of observations	0	12	21	3
Peregrine				
Average distance to nearest nest		468	180	330
Nearest recorded nest		ca400+	10	200
Number of observations		8	63	3
Rough-leg				
Average distance to nearest nest			550	387
Nearest recorded nest			ca400+	200
Number of observations			6	3
Raven				
Average distance to nearest nest				0
Nearest recorded nest				0
Number of observations				0

*Measurements in yards.

TABLE 6

Description of Twenty-seven Nesting Sites Used by Gyrfalcons in 1967, 1968, and 1969 on the Colville River

Cliff number	*Number of years used*	*Vertical measurements in feet*			*Type of aerie site*
		Above river	*Below brink*	*Above base*	
20	3	40	30	30	Old Rough-leg nest on overhung ledge.
28	2	60	5	15	Old stick nest (Raven?) under projecting slab of shale.
41	1	60	10	20	Old stick nest (Raven?) under projection of shale.
41	2	250	20	25	Stick nest used by Rough-leg in 1967. Vertical face with slight overhang.
44	1	80	6	80	Rough-leg nest of 1967. Sheer cliff with brushy overhang.
45	1	50	12	40	Stick nest (Raven?) with slight overhang on sheer wall.
45	1	60	30	—	Ledge on vertical face with slight overhang.
45	1	50	5	25	Stick nest on shelf under slight overhang.
47	2	70	5	70	Stick nest under projection of shale.
48	3	200	6	15	Stick nest under sandstone overhang.
52	2	100	50	12	Stick nest under overhang on sheer wall.
53	2	20	100	20	Scrape in a notch on sheer wall with overhang.
53	1	20	5	6	Stick nest with brushy overhang.
54	1	50	200	50	Sheer wall to river. Stick nest used by Ravens in 1968 with extreme overhang.
54	1	50	100	50	Scrape on deep ledge under overhang.
57	1	75	15	15	Stick nest (Raven?) on slab with overhang on vertical face.
58	2	300	5	15	Ledge with prominent jutting overhang on sheer face.

same cliffs as falcons do in order to use the remains of food killed by the falcons and thus act as commensals. Of 18 Raven nestings between 1967–1969, five were on cliffs with Gyrfalcons and eight on cliffs with Peregrines.

Perhaps our most surprising finding is the density of nesting Gyrfalcons and the numbers of ptarmigan they took as prey. We saw and heard few ptarmigan in the Colville valley proper—less than 20 individuals in 1967 on the entire stretch of the Colville and less than 10 in 1968 and 1969. In the uplands, however, there were more ptarmigan, especially in 1967. The following example, taken from our 1967 notes, shows the pattern of ptarmigan distribution.

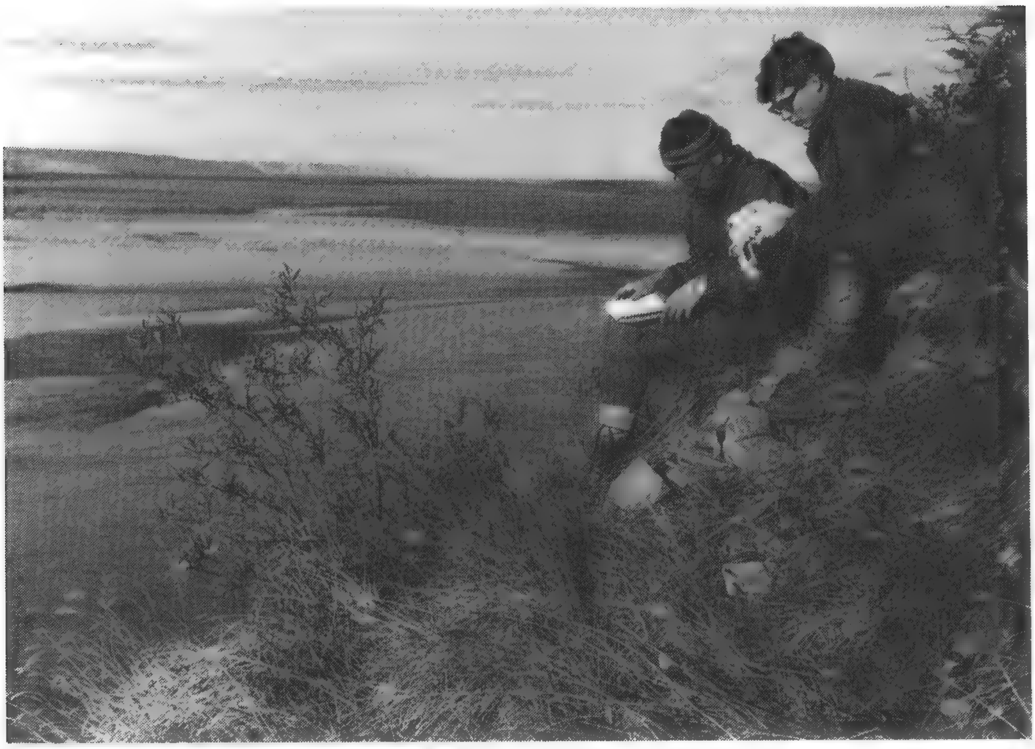


Figure 12. Peregrine aerie site near Umiat, Alaska. The scrape was in grass on the upper side of the willow in the foreground, easily accessible from the top of the cliff. One of the young falcons being banded in this picture on 29 July 1969 was reportedly caught by a falconer on a beach in Los Angeles, California, on 9 October of the same year.

We saw an adult male Willow Ptarmigan (*Lagopus lagopus*), probably the same bird, two or three times at the Etivluk camp in June; we heard two males at Umiat in June; and at least two males were present near Ocean Point at the end of June and the first of July. In August there were two males and a female near the camp at Ocean Point, and across the river in the willows we flushed a flock of six adult males and a pair with four flying young. We saw no Rock Ptarmigan (*Lagopus mutus*) at all. Evidently Gyrfalcons ranged far afield for ptarmigan that year. We think they found them mainly in the highlands between the Colville River and the coastal plain to the north, such as around Knifeblade Ridge and Lookout Ridge. When we made aircraft flights over these areas in early June, we saw male Willow Ptarmigan rather often. For instance, on a flight from Barrow to the Etivluk and return on June 8 we spotted — in 188 minutes of travel from the Meade River Camp to the Colville and back to Maybe Creek — 105 spaced-out male Willow Ptarmigan, or one male per three linear miles over a quarter-mile-wide sweep at a density, possibly, of one pair per square mile.

When ptarmigan are present even in only moderate numbers, they are very conspicuous in the flood plain of the river. In 1964, White found about 18 territories of ptarmigan in 6.5 square miles around Umiat, showing how dense they can be. Apparently, in 1967, 1968, and 1969 Gyrfalcons traveled some distance from their aeries to a region, unknown to us, to obtain ptarmigan. We found no evidence of starving young falcons as Cade (1960) found in 1957, and yet the ptarmigan population in the river valley appeared to be no higher in 1967, 1968, and 1969 than it was in 1957.

The food data clearly suggest that there may be no competition, not even a serious overlap, for the available food resources. Competition for food might develop where there are low populations of resident prey, such as ptarmigan or microtines. In poor ptarmigan years, Gyrfalcons might compete with

Rough-legs for mammals, especially if microtines were also low (note in Table 8 the high percentage of microtines taken by Gyrfalcons). Both Gyrfalcons and Rough-legged Hawks do shift with some degree of efficiency to migrant birds, but we doubt whether they would be very successful in raising their broods on a diet mainly of migrants. For example, White noted in 1964 that Gyrfalcons shifted over to a diet of plover (*Squatarola squatarola* and *Pluvialis dominica*) and ground squirrels, chiefly the latter, in late June when there was a sudden weather-induced exodus of ptarmigan from the foothills of the Colville region. Both species apparently adjust to the lack of suitable prey by simply not breeding or by reducing clutch size.

The extremely wide versatility of Peregrines in taking prey species would seemingly obviate competition with other raptors for any food resource on the Arctic Slope. In the 1967–1969 seasons, 17 per cent of the Peregrines' food consisted of "willow-inhabiting" passerines—Gray Jay (*Perisoreus canadensis*) thrushes, warblers, and three species of finches. These same species comprised 15 per cent of the Peregrines' food on the Colville in 1952 (Cade, 1960). None of 245 bird prey items of Gyrfalcons on the Arctic Slope between 1952 and 1959 (Cade, 1960) and none of 981 bird prey items in 1967–1969 were of willow-inhabiting passerines. Because of their small size, these species are probably more easily exploited by Peregrines, especially by the smaller males. This food resource, the vast range of migrant passerines and shorebirds, is nearly untouched by Gyrfalcons. Just the reverse condition exists with small mammals. In 1967–1969 only about one per cent of the Peregrines' food consisted of rodents as compared with about four per cent in 1952 (Cade, 1960). Gyrfalcon food items in 1967–1969 consisted of four per cent rodents compared to about nine per cent between 1952–1959 (Cade, 1960). Rodents are, however, more important in the diet of the Gyrfalcon than the "remains" indicate. The analysis in Table 8 does not include large numbers of pellets consisting of rodent fur, found at Gyrfalcon nests.

Perhaps we should treat the food data another way. Ptarmigan made up 91 per cent of the Gyrfalcons' prey in 1967–1969 and 45 per cent in 1952–1959 (Cade, 1960). In 1967–1969, rodents made up almost half, 48 per cent, of the bird and animal food items, excluding ptarmigan. The same treatment with the Peregrine's prey has little meaning as no one food species makes up the bulk of its diet.

As mentioned earlier, the reproductive performance of Rough-legged Hawks reflects the population densities of microtines. Hawks also catch a considerable number of birds, especially fledglings and post-breeding adults in heavy wing molt. In previous years Rough-legs along the Colville have occasionally fed rather heavily on young ptarmigan and on arctic ground squirrels (*Spermophilus undulatus*), but their breeding density and reproductive success are most responsive to the numbers of microtine rodents. In 1957, for instance, when microtine populations were the lowest, we recorded only seven pairs of Rough-legs nesting on the 17 cliffs between the Oolamnagavik and Umiat Mountain, where as many as 21 pairs have bred in one season, and the hawks turned to alternate forms of prey. In 1959, a good year for microtines especially upriver from Umiat, Cade recorded 58 pairs of Rough-legs along the whole length of the river, and 14 of these nested between Oolamnagavik and Umiat Mountain.

By analyzing hawk food remains, one also obtains an overview of the differences in densities of the five species of microtines, namely, brown lemming (*Lemmus trimucronatus*), collared lemming (*Dicrostonyx groenlandi-*

cus), tundra vole (*Microtus oeconomus*), Alaska vole (*Microtus miurus*) and red-back vole (*Clethrionomys rutilus*). For example, 1968 was a big year for the collared lemming while, in 1969, we found none as food remains (see Table 10).

Discussion

As we are mainly concerned with the adjustments of sympatric species to avoid competition and with an assessment of the degree of overlap in the use of niches by raptors in a faunistically simple environment, we focus our concluding remarks on points that demonstrate habitat partitioning, differential use of prey species, and other ecological traits that reflect similarities and differences among cliff-nesting raptors in arctic Alaska.

Four species of medium-sized predaceous birds nest on cliffs along the Colville River in northern Alaska. The Gyrfalcon is essentially a resident arctic species, specializing on ptarmigan for its food. The Peregrine Falcon is a transcontinental migrant breeding in the far north and wintering mainly south of the United States, as far as Argentina. It feeds on a wide variety of birds, chiefly migrant passerines, shorebirds, and waterfowl, and, in years when ptarmigan are abundant, it preys heavily on them too.

The Rough-legged Hawk, a migrant that does not move as far south as the Peregrine, is a microtine rodent specialist, but it can also shift to other prey, such as ground squirrels and birds, when microtines are scarce. The Raven, a year-round resident in arctic Alaska, is functionally a "raptor" that feeds partly on carrion and partly by hunting live prey.

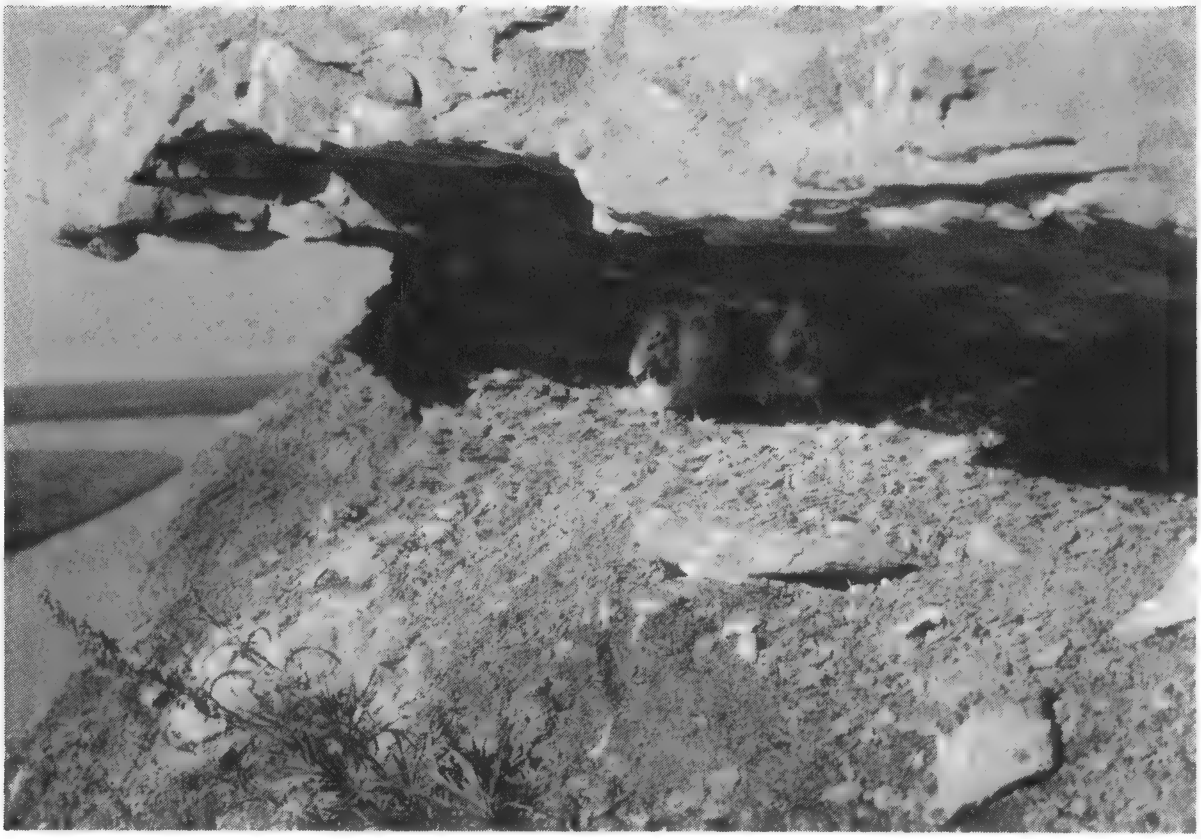


Figure 13. Peregrine aerie site on a deeply recessed ledge on a tall, rocky cliff along the upper river. 1 August 1967. From a kodachrome by W. R. Spofford.

We have studied these birds intensively on a 183-mile stretch of the Colville River, from the mouth of the Etivluk River to Ocean Point, during the breeding seasons of 1967, 1968, and 1969. In addition, we carried out more extensive studies covering all or parts of this stretch in earlier years, 1952, 1956 through 1959, and 1964. Our conclusions are based on information from more than 60 Gyrfalcon, 215 Peregrine, 480 Rough-leg, and 37 Raven nestings.

Body Size

Storer (1966) studied the size relationships among the three species of North American accipiters and made an interesting case for sexual size dimorphism to function as a mechanism that reduces interspecific and intraspecific competition for food. The rationale for such an explanation is that the size of a raptor sets certain limits to the size of its prey. Obviously if the prey is too large, the raptor cannot subdue it. The lower limit is determined by the smallest sized prey from which the raptor can obtain more energy than it has to expend in capturing it. It also follows that there should be an optimum prey size or range of prey sizes for each raptor body size. Theoretically, two raptors the same size should be adapted to catch much the same kinds of prey unless they are specially modified in some other way — differences in feet, wings, beaks, and so on. The same body size would place similarly adapted raptors — either a pair or individuals of two sympatric species — in a position of potential or actual competition. Interspecifically, two similar species can solve this problem by some kind of habitat partitioning, using different habitats, the same habitat at different times, or different portions of the same habitat. The problem can be solved intraspecifically either by the existence of a large variation in size or other individual differences correlated with feeding differences, by different wintering ranges for males and females or adults and young, by territoriality, or by some other form of habitat partitioning (see Selander, 1966, for many examples); but when the sexes have to come together for breeding and remain together in a confined area for a long period of time, only some form of differential niche use can reduce intraspecific competition. As Storer (1966) demonstrated for the accipiters and Selander (1966) for woodpeckers and other species, a sexual difference in body size is one way to promote differences in food habits between males and females.

Storer's analysis of the size relations among the North American accipiters is compelling. We agree that the sexual differences in size can result in average differences in the sizes of prey taken by males and females, but we feel that Storer's explanation for the adaptive value of sexual size dimorphism is not quite correct.

Before pursuing this interesting question further, we should point out that sexual size dimorphism may be an evolutionary modification for some adaptation entirely unrelated to feeding. Cade (1960) and others (Brown and Amadon, 1968) discussed various theoretical considerations. We feel, however, that the relationship between body size and food niche is germaine to our consideration of the Colville raptors, especially the Gyrfalcon and the Peregrine.

There is a size range among the four cliff-nesting species along the Colville. Because of the larger samples, we mainly rely on the wing length as an indicator of size in the following considerations. Arctic American Peregrines show no size overlap with Ravens and Rough-legs, and there is a 3.9 per cent

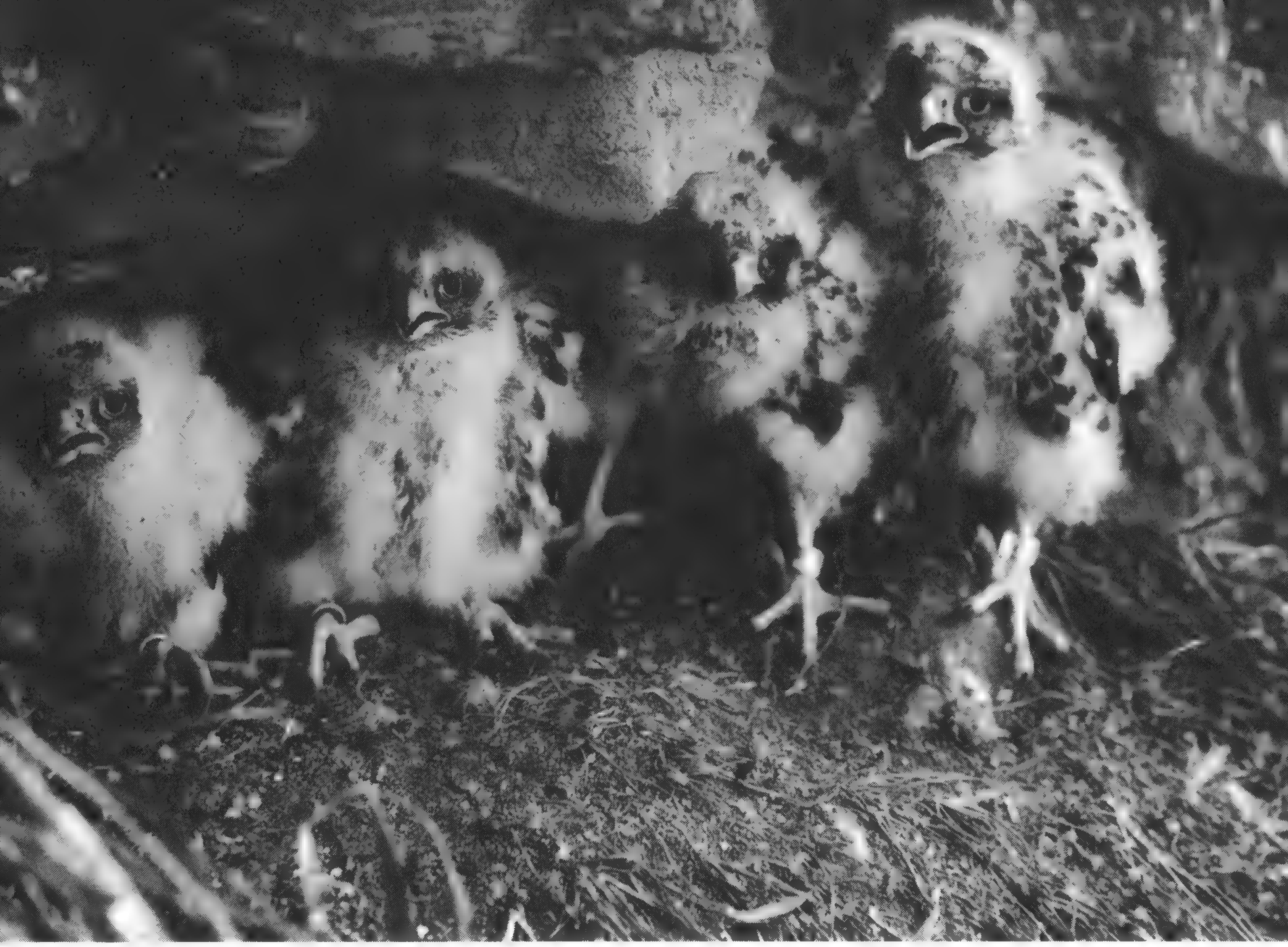


Figure 14. Banded young Peregrines in an aerie on a slightly recessed ledge. 2 August 1967. From a kodachrome by W. R. Spofford.

area of non-overlap between arctic male and female Peregrines in the total range of wing lengths for both sexes. Female Peregrines show no size overlap with female Gyrfalcons and only a 19 per cent overlap with male Gyrfalcons. Male and female Gyrfalcons show a 12 per cent overlap in wing length. Gyrfalcons have a 31 per cent overlap with Rough-legged Hawks; the foods they share in common are ptarmigan and, especially, microtine rodents, but there is no doubt that the two species of raptors hunt these prey in different ways and to different degrees. Here the obvious differences in wing-loading (Table 1) and other characteristics of flight become important. There is a 4.9 per cent overlap between large female Gyrfalcons and small male or female Ravens. Since Ravens take such a wide variety of food, both carrion and living prey, and no doubt exploit ptarmigan and rodents differently than Gyrfalcons — indeed, they may be significantly dependent upon Gyrfalcons for carrion — the overlap in body size between the two can have little significance in terms of competition for food. Male and female Rough-legs have a 23 per cent overlap, and Rough-legs overlap with Ravens 36 per cent. Moreover, the wing-loading characteristics of these two species are very similar. They both feed heavily on microtine rodents, as do a number of other arctic, sympatric, predatory birds — owls, jaegers, and gulls — but probably their methods of hunting differ so strikingly that, in terms of prey vulnerability, they essentially feed on two separate classes of microtines. This is a point that must be verified by detailed observations on how Ravens hunt. Finally, Ravens show the greatest degree of intraspecific sexual size overlap, with males averaging larger than females by 48 per cent. It is interesting to note that scavenging falconiform species also show little or no sexual size dimorphism.

TABLE 7

Description of Twenty-five Nesting Sites Used by Peregrine Falcons along the Colville River in 1967

Cliff number	Vertical measurements in feet			Type of aerie site
	Above river	Below brink	Above base	
1	100	50	100	Earth platform on break in slope above rock face.
7	90	15	90	Ledge under slight overhang on vertical rock face.
9	250	30	30	Earth scrape on nose of rocky promontory.
12	90	5	90	Shale ledge just below brink, willow shrub screen.
14	30	10	30	Shale ledge under slight overhang, forb screen.
28	72	2	—	Platform on gentle break in slope. No sheer drop for 20 feet.
41	100	30	10	Old stick nest on ledge of vertical rock face.
44	80	75	80	Below nose of outcrop under sharp undercut of rock.
48	200	10	35	Ledge under slight overhang on face of rock pinnacle.
52	200	40	0	On ledge 20 feet below a rocky nose.
53	120	20	0	On a walk-in nose near upland.
54	100	60	100	Grassy area at break in slope above vertical face.
57	150	30	?	On shelf above a low vertical face.
58	30	75	30	Pothole on vertical face.
59	200	20	75	Scrape at brink of brushy slope.
60	200	—	—	Platform on knifeblade ridge of dried mud.
63	100	100	—	Platform on knifeblade ridge of dried mud.
63	150	100	—	Platform on knifeblade ridge of dried mud.
63	100	150	—	Platform below a break in slope, knifeblade ridge.
64	75	100	—	On knifeblade ridge of dried mud.
68	150	5	150	Grassy ledge on earth-mud face.
68	50	50	—	Grassy area on steep mud ridge.
72	80	?	?	Grassy point at break in slope of mud-earth bluff.
79	40	30	40	Grassy nose at break in slope of mud-earth bluff.
80	40	20	40	Grassy nose at break in slope of mud-earth bluff.

TABLE 8

Prey of Gyrfalcons Found at Nests along the Colville River

Species	*Number found**		
BIRDS	1967	1968	1969
Canada Goose, young (*Branta canadensis*)	1		
Pintail (*Anas acuta*)		3	
Green-winged Teal (?) (*A. carolinensis*)	1		
Greater Scaup (*Aythya marila*)	1		
Old Squaw (*Clangula hyemalis*)	3	1	1
Rough-legged Hawk (*Buteo lagopus*)	1		
Ptarmigan, spp (*Lagopus* spp)	246	108	208
American Golden Plover (*Pluvialis dominica*)	1		
Common Snipe (*Capella gallinago*)			1
Whimbrel (*Numenius phaeopus*)	1		
Jaeger, spp (*Stercorarius* spp)			1
Glaucous Gull (*Larus hyperboreus*)	1		
Short-eared Owl (*Asio flammeus*)	9		1
Lapland Longspur (*Calcarius lapponicus*)	1		
Unidentified passerine			1
Total birds	266	112	213
MAMMALS			
Shrew, sp (*Sorex* sp)	1		
Arctic ground squirrel (*Spermophilus undulatus*)	1		5
Tundra vole (*Microtus oeconomus*)			1
Other microtine rodents	15	1	3
Total mammals	17	1	9
TOTAL PREY	283	113	222

*Not included in the count are many pellets, composed mainly of microtines, from many nests and several remains of fresh, bloody ptarmigan on each of two nest ledges.

Because Peregrines are more closely related and more similar in ecological function to Gyrfalcons, one would expect the most competitive interaction between these two species. Following Storer's analysis of the accipiters, the differences in size of male and female Peregrines and Gyrfalcons could be related to the use of different size prey. Our observations indicate clearly that male Peregrines take a higher percentage of passerines and small to medium-sized shorebirds than females do; the females take a higher percentage of medium to large-sized shorebirds and waterfowl (see Cade, 1960). Male and female Gyrfalcons both take ptarmigan and ground squirrels readily. We suspect that they are about equally adept at catching waterfowl, but we lack observations on wild falcons. Also we do not know whether one sex has a greater tendency to catch microtines than the other; but we believe it is safe to conclude that there is much less difference in the food habits of male and female Gyrfalcons than there is between male and female Peregrines, yet the

TABLE 9

Prey of Peregrine Falcon Found at Nests along the Colville River

Species	*Number found*		
BIRDS	1967	1968	1969
Arctic Loon, large downy young (*Gavia arctica*)		1	
Canada Goose, goslings		4	
Pintail	1		2
Green-winged Teal	1		1
American Widgeon (*Mareca americana*)	1		
Greater Scaup	2		
Red-breasted Merganser (*Mergus serrator*)		1	3
Scoter, sp?	1		
Unidentified waterfowl		2	1
Ptarmigan, spp	5	3	6
*Rough-legged Hawk			4
**Peregrine Falcon			2
Semipalmated Plover (*Charadrius semipalmatus*)	4	1	4
American Golden Plover	6	8	16
Common Snipe	8	7	22
Spotted Sandpiper (*Actitis macularia*)		1	2
Lesser Yellowlegs (*Totanus flavipes*)	1	1	
Pectoral Sandpiper (*Erolia melanotos*)			4
Long-billed Dowitcher (*Limnodromus scolopaceus*)	2	3	4
Semipalmated Sandpiper (*Ereunetes pusillus*)		1	
Bar-tailed Godwit (*Limosa lapponica*)	1		
Northern Phalarope (*Lobipes lobatus*)	7	2	3
Unidentified shorebirds	4	10	4
Parasitic Jaeger (*Stercorarius parasitacus*)	6	2	34
Long-tailed Jaeger (*S. longicaudus*)	6	1	2
Pomarine Jaeger (*S. pomarinus*)			1
Unidentified jaegers	2	5	10
Sabine's Gull (*Xema sabini*)	2		
Unidentified gulls	2		1
Arctic Tern (*Sterna paradisaea*)		1	1
Short-eared Owl	4	1	2
Say's Phoebe (*Sayornis saya*)	1	1	1
Gray Jay (*Perisoreus canadensis*)	1	1	
Gray-cheeked Thrush (*Hylocichla minima*)	5	5	10
Bluethroat (*Luscinia svecica*)			1
Arctic Warbler (*Phylloscopus borealis*)	1	2	3
Yellow Wagtail (*Motacilla flava*)	13	7	14
Water Pipit (*Anthus spinoletta*)			1
Northern Shrike (*Lanius excubitor*)	1	1	
Yellow Warbler (*Dendroica petechia*)	1		3
Redpoll, sp (*Acanthis* sp)		1	1
Tree Sparrow (*Spizella arborea*)	9	3	10
White-crowned Sparrow (*Zonotrichia leucophrys*)	1	1	2
Fox Sparrow (*Passerella iliaca*)	9	8	3
Lapland Longspur	4	3	15
Unidentified passerines	20	10	10
Total birds	133	97	203
MAMMALS			
Arctic ground squirrel			1
Alaska vole (*Microtus miurus*)		1	
Other microtine rodents	2		
Total mammals	2	1	1
TOTAL PREY	135	98	204

*Juvenile.

**Siblings, either killed or died and eaten.

degree of sexual difference in size is only slightly less in Gyrfalcons than it is in the tundra Peregrines, especially in body weight. The difference in wing-loading is actually greater between male and female Gyrfalcons than between male and female Peregrines, just the reverse of what one would predict from the known feeding habits.

Peregrines, mainly females, do take ptarmigan — significantly so in peak years; Gyrfalcons do take waterfowl, especially late in the nesting season and in years when ptarmigan are scarce. Thus, there *is* overlap in the species of prey taken by these two falcons, but it is doubtful whether either species ever makes an important impact on the "special" food of the other. Serious competition for food is unlikely between these species, except perhaps occasionally between individual pairs. Again, the vulnerability of individual ptarmigan and waterfowl may be different for Gyrfalcons than for Peregrines. In summary, if size is important in reducing competition for food sources among any of the Colville raptors, then the size differences between the two species of falcons are most likely to be significant. Even so, the habits of Gyrfalcons and Peregrines are distinct enough in other respects so that food selection could be different regardless of the size differences.

Returning to the significance of sexual size dimorphism among the four Colville species, only the Peregrine shows a clear difference in feeding habits between males and females, a difference that can be associated with the markedly smaller size of males compared to females. This species provides another example of the correlation between body size and prey size that Storer (1966) has worked out in detail for the accipiters, the selective value being decreased competition for food between the sexes according to his view. Storer seems to doubt whether these sexual differences could have adaptive value during the breeding season, evidently having been influenced by some earlier criticisms (Cade, 1960), the reasons being because the male provides most of the food for the female and young during the breeding season and because food is most abundant during this period. He feels that the selective advantage is more likely to operate in the wintering quarters where food may be sparse and where competition between the sexes and with resident hawks taking similar food would favor increased sexual size dimorphism.

There is little that we can say about conditions on the wintering grounds of the tundra Peregrine. It is problematical whether food is less available in the Neotropics than in the Arctic, or whether, except for the South American populations of Peregrines, there are potential resident competitors. Generally speaking, wintering hawks and falcons keep to individual feeding areas or "territories," and with this kind of spatial partitioning of the environment, it is difficult to see how there could be much selection for sexual size dimorphism as a response to intraspecific food competition.

If selection has actually worked on size dimorphism as a primary feeding adaptation, then we feel its relevance is mainly during the breeding season, for the following reasons: It is then only that the male and female coinhabit a restricted area around the nest site and therefore make the heaviest demands on a local supply of prey. While it is true that the male Peregrine feeds the female during incubation and also during roughly the first half of the nesting period, as well as the nestlings themselves, actually the female becomes an important provider of food during the latter part of the nestlings' life and during the fledglings' period of dependency. We believe the size dimorphism and related food habits could have been selected as a way of maximizing the ability of a pair of falcons to exploit a local, mixed species population of birds for rearing their young. Just at the time when the male may have about exhausted the supply of vulnerable prey in his optimum size class and within his range of efficient operation from the nest, the female is released from her brooding and guarding duties at the aerie. She can begin to exploit the vulnerable birds in her size range. Such an arrangement should result in the maximum production of young, irrespective of any potential competition between the male and female.

The key considerations in this explanation are (1) prey vulnerability and (2) the maximum effective hunting range. The hunting range of a hawk or falcon with a brood must be limited by a distance beyond which it cannot make a sufficient number of deliveries to sustain the young even if the hunting continues to be successful in peripheral areas. We do not know what this distance is for any hawk, but it sets a limit on the available prey, a limit that is independent of prey density. Within this effective operating range, not all suitable prey are equally vulnerable to capture, and once a hawk has caught

TABLE 10

Prey of Rough-legged Hawks Found at Nests along the Colville River

Species	*Number found*		
BIRDS	1967	1968	1969
Loon, sp		1	
Greater Scaup	1		
Unidentified duck		1	
Rough-legged Hawk	1		1
Willow Ptarmigan (*Lagopus lagopus*)	1		
Ptarmigan, spp		2	
Northern Phalarope	1		
Say's Phoebe	1		
Bluethroat		2	
Yellow Wagtail			3
Tree Sparrow	1	2	1
Lapland Longspur			1
Unidentified large bird	1		
Unidentified passerine		1	1
Total birds	7	9	7
MAMMALS			
Arctic ground squirrel	3		3
Brown lemming (*Lemmus trimucronatus*)	9	17	11
Collared lemming (*Dicrostonyx groenlandicus*)	4	20	
Red-back vole (*Clethrionomys rutilus*)	4	1	2
Alaska vole	5	10	6
Tundra vole	7	5	18
Unidentified or unspecified voles		20	3
Total mammals	32	73	43
TOTAL PREY	39	82	50

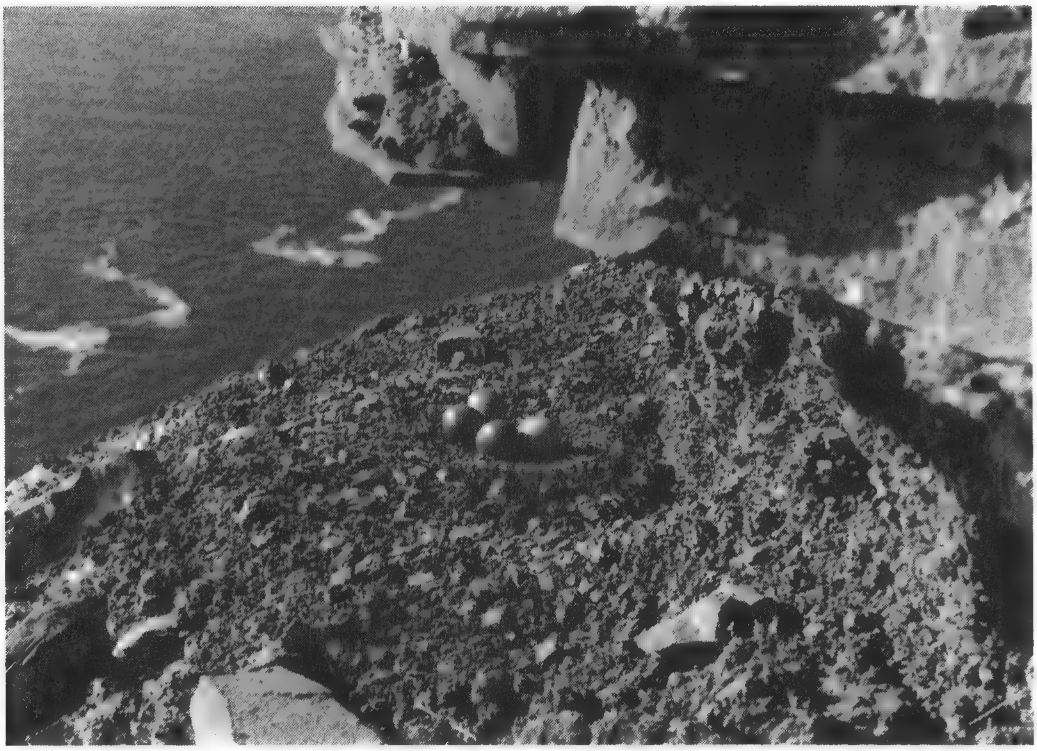


Figure 15. Gyrfalcon's nesting ledge on the upper river. Note the deep recess. This scrape is unusual in that it was made in bare, rocky chips with no trace of a stick nest. 12 June 1967.

the vulnerable individuals, it will have to work proportionately longer and harder to effect a capture even though prey density *per se* may still be high.

In this regard, also, let us compare the differences in the feeding regimes of breeding Peregrines and Gyrfalcons. Female Gyrfalcons leave their young unbrooded at the age of three weeks or less when they are still downy — at a much earlier stage than female Peregrines do—and they join the males in hunting, chiefly for ptarmigan. The adults leave the vicinity of the nesting cliff completely and presumably hunt far away. From this time on, neither adult Gyrfalcon is ever at the aerie longer than a few minutes at a time — usually just long enough to deliver prey and feed the young. The Gyrfalcons have adapted to the problems of feeding their young by specializing heavily on one type of prey, ptarmigan, by increasing the amount of time both parents hunt simultaneously, and presumably by ranging farther away from the nest than Peregrines do. The added range is made possible by the simultaneous hunting by both parents, by their larger size, heavier wing-loading, and faster flight.

None of these explanations accounts for the reason why the female sex is the larger among falconiforms. The primary adaptation for the "reversed" sexual size dimorphism in these birds is almost certainly related to that function, whatever it is, while the feeding associations are secondary (Cade, 1960; Brown and Amadon, 1968).

Nesting Habits

Since the four Colville species have specific requirements for nesting on cliffs and, as far as we know now, only on cliffs in arctic Alaska, we can predict that the geographic occurrence of cliffs determines the distribution and also, to some extent, the density of the breeding pairs. Obviously, where there are no cliffs, there will be no cliff-nesters. For this reason, breeding Gyrfalcons, Peregrines, Rough-legged Hawks, and Ravens do not occur widely over the arctic coastal plain of Alaska. On the other hand, the converse proposition does not hold — that wherever there are cliffs, there are cliff-nesters; and this fact presents an unresolved problem requiring further study. Again, it is rather obvious that altitudinal effects in the Books Range will intervene, rendering many of the magnificent escarpments there unsuited for nesting by these birds. Peregrines and Rough-legs reach their altitudinal limits around 2,500 to 3,000 feet. It is doubtful that Gyrfalcons or Ravens nest much above 3,500 to 4,000 feet.

What is not so clear is why some cliffs within the optimum range for breeding seem never to be used. Of the 80 cliffs listed in Table 2 for the Colville, nine have never been used by any species during the nine years of our observations. Particularly puzzling is the stretch of river that includes Cliffs 17 through 25, only two of which have been occupied by breeding raptors or Ravens. Yet breeding birds commonly occupy cliffs both upriver and downriver from this sector. Part of the problem undoubtedly lies in the inability of a human observer to judge the suitability of a particular cliff as potential nesting habitat. This is less true for Peregrines and Rough-legged Hawks, which manifest wide acceptability for nesting sites, than for Gyrfalcons and Ravens whose choice of sites is determined by snow conditions prevailing on the cliffs before our observations begin.

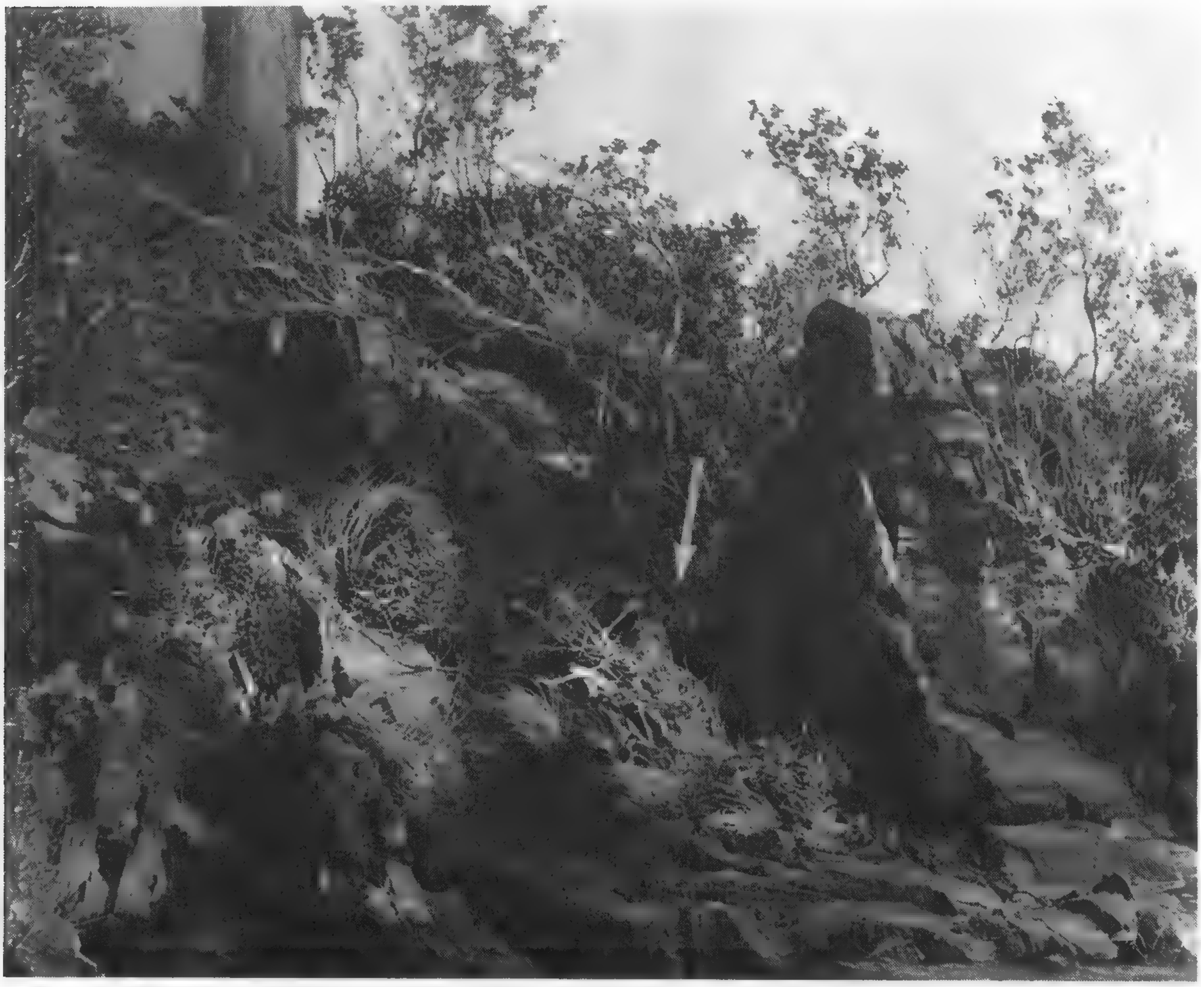


Figure 16. Typical low Gyrfalcon's site (below white arrow) on the upper river, with projecting slab of rock protecting a deeply recessed ledge. Gyrfalcons bred successfully at this site in 1967 and 1968, utilizing an old stick nest; Ravens occupied the exact site in 1969. 6 July 1967.

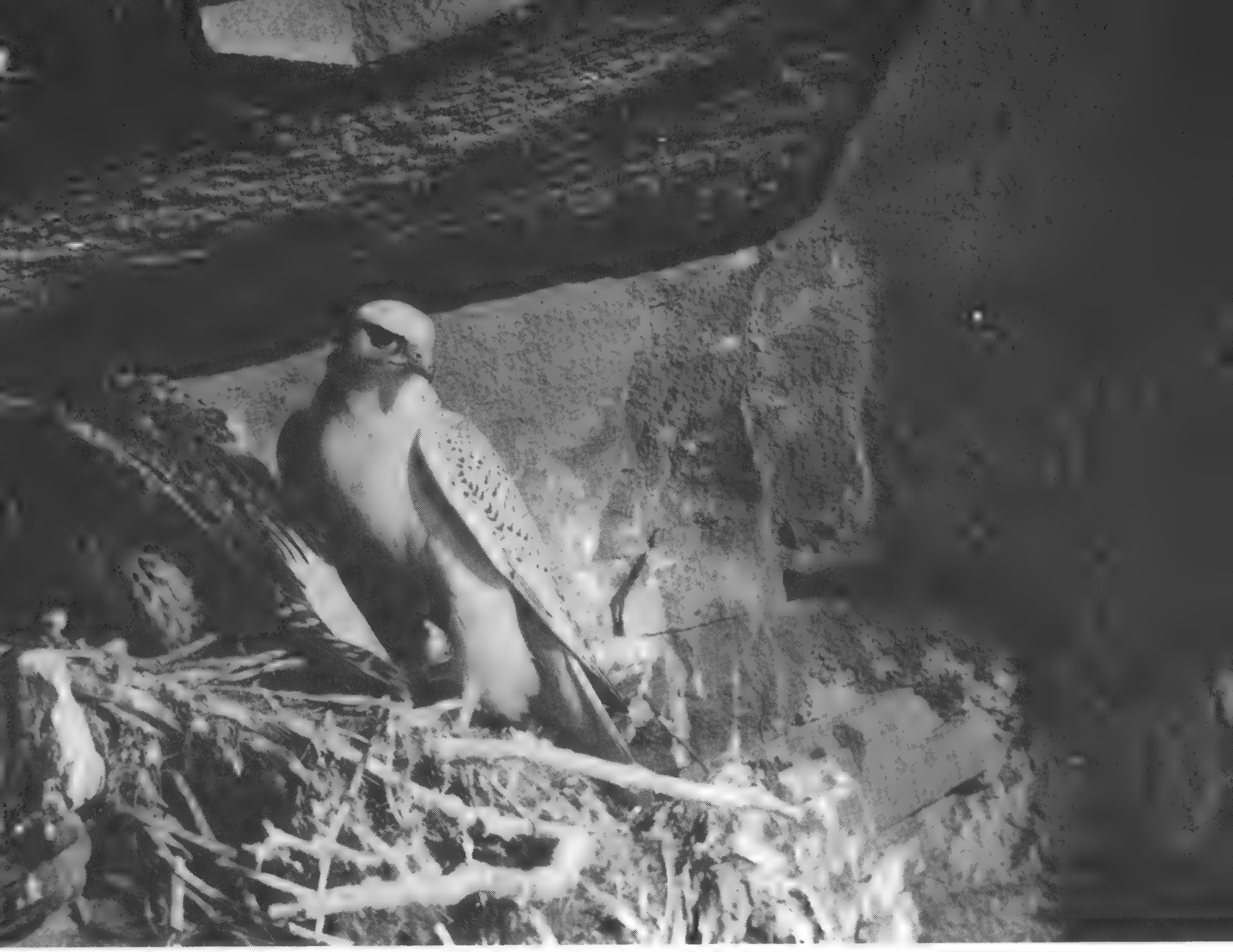


Figure 17. Adult male Gyrfalcon at an aerie on the upper river. The stick nest probably was an old Raven's. This white tiercel nested at this cliff in 1967, 1968, and 1969; he was mated with a very dark gray female. 9 July 1967. From a kodachrome by W. R. Spofford.

We conclude that a suitably protected substratum is what the Ravens and Gyrfalcons choose in selecting a nest site and that the presence of other raptors exerts little influence on their choices. It is on hard rock that ledges and overhangs are most apt to form and endure, and this type of formation determines where Gyrfalcons and Ravens nest. If Gyrfalcons do make choices on the basis of substratum rather than on the position or absence of other active nests of hawks or Ravens, this would explain why Gyrfalcon distribution ends where "hard" rock gives out downriver. Certainly ptarmigan and microtines are present downriver. Thus, we cannot consider food a factor limiting their distribution in the coastal plain.

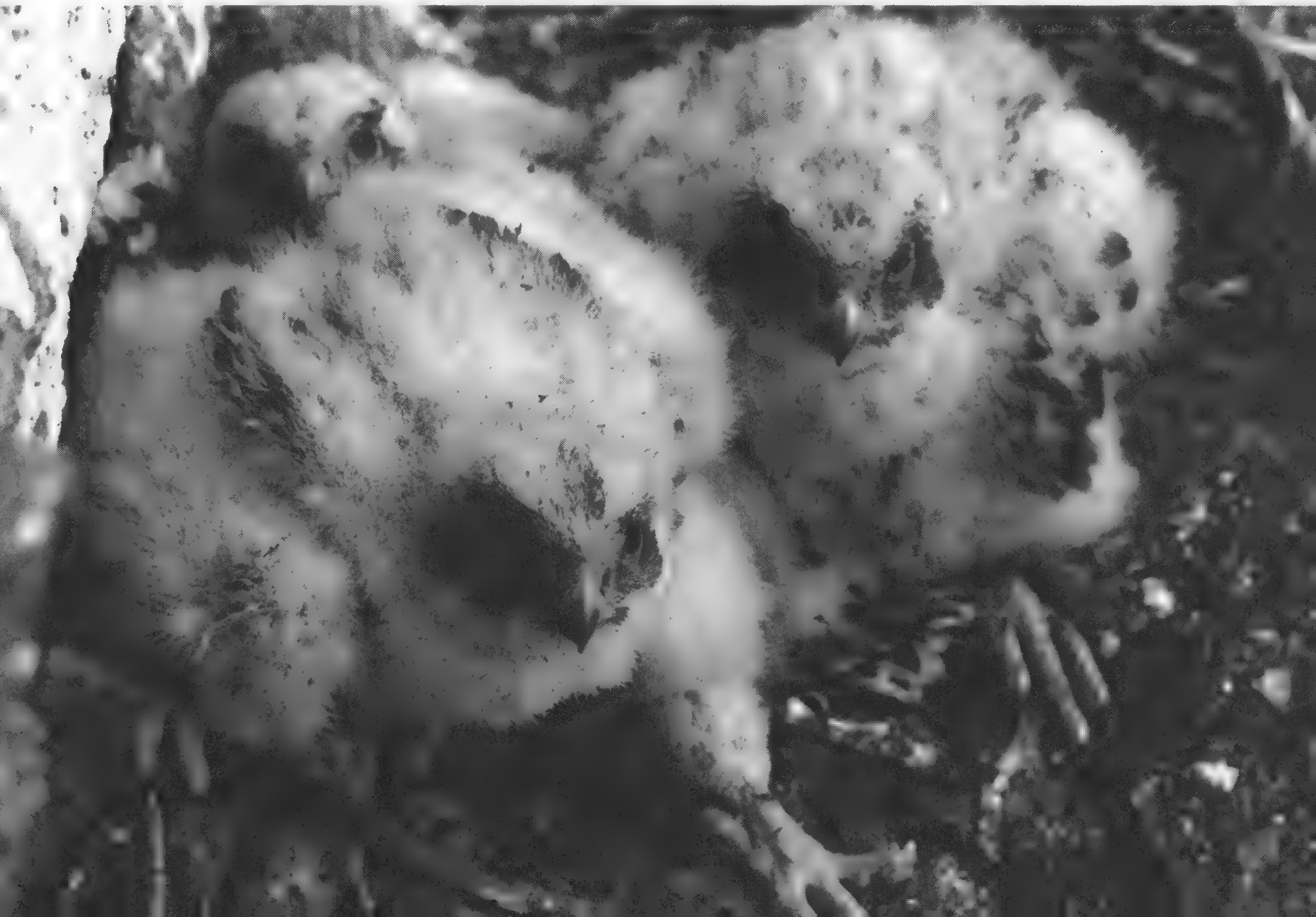
In the years when Rough-legged Hawks and Gyrfalcons reach maximum densities along the Colville, as in 1959, and 1967 to 1969, their breeding populations appear to come close to an occupancy of all the available nesting habitat; in other years they obviously do not. On the other hand, the number of breeding pairs of Peregrines and Ravens has always been far below the number that we could have predicted on the basis of available nesting habitat. Some factors other than the geographic availability of nesting habitat must, therefore, influence the density of all these populations.

The tendency for historical occupancy and tenacity in the use of nesting sites may act both to produce and eliminate competition. That is to say, if nesting sites are too close to one another, then each year some sort of interaction or conflict will occur until each pair makes the appropriate adjustments. Clearly, closely nesting pairs never completely adjust. In 1968, we observed terrific aggression between the Peregrines and Rough-legs at Cliff 28 where the two nests were only 10 yards apart. The level of aggression was apparently more or less constant throughout the season, at least until we left, although the level of observed aggression may have been a function of human presence. Despite the aggression both pairs produced young. More often than not, however, the distances between sites tend to be adjusted to values that lower or produce minimal aggression. Therefore, we suggest that traditional use of these sites will in the long run, or in the historical sense, reduce the total impact of intolerant behavior and promote stability in the populations.

With few exceptions the various species do not place their nests in view of one another. The exceptions tend to be among the Rough-legs in that they can sometimes sit on their nests and look directly into the nesting site of a falcon, and occasionally the reverse occurs. In 1964, White, sitting at a Peregrine aerie near Umiat, could see the flapping wings of nearly fledged Gyrfalcons; however, when he crouched down by the Peregrine scrape, the Gyrfalcons disappeared from view. We are tempted to suggest that Peregrines and Gyrfalcons can live on the same cliff if their nests are not visible to one another and if their schedules or routes of going to and from their nests to hunt are different. When they can see each other on their nests, and when coming and going to the cliff, friction results (See Cade, 1960, for an example).

Previously Cade (1960) thought that competition was important between Peregrines and Gyrfalcons. In earlier years it seemed that, when Gyrfalcons were less numerous, Peregrines were more common and *vice versa*; but by 1959, it was evident that the two species could occupy the same cliff simultaneously and successfully. We substantiated this fact by additional cases in 1964,

Figure 18. Brood of young Gyrfalcons, about four weeks old. These birds had already been left unbrooded by the female for a week or more. 3 July 1967.



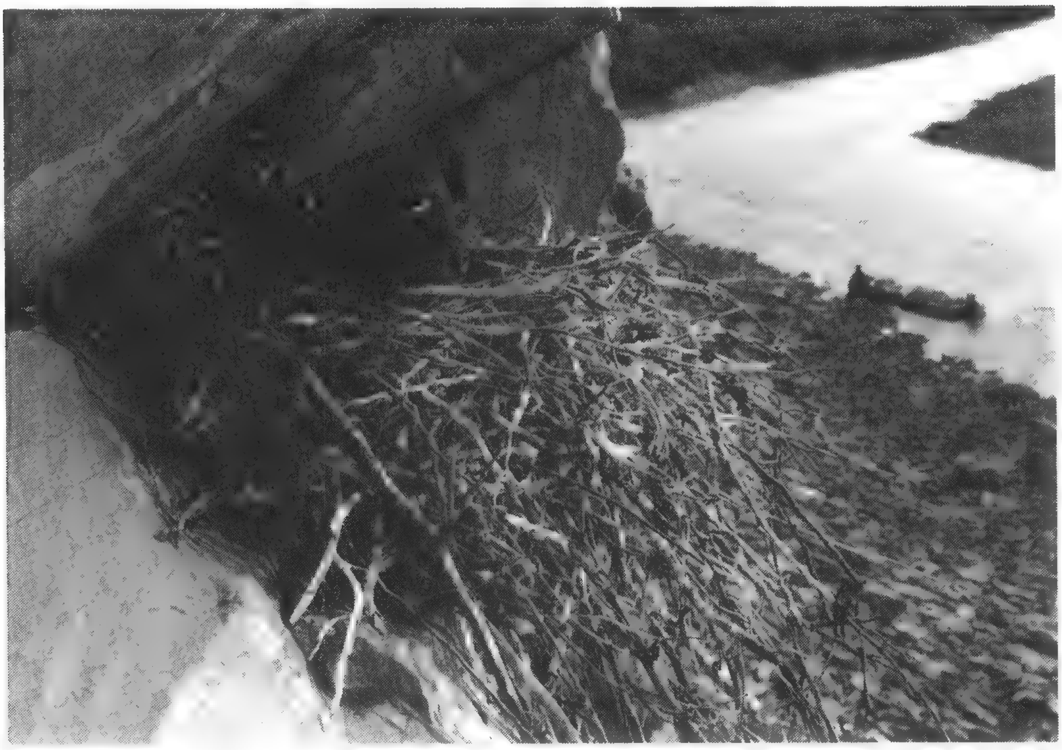


Figure 19. Young Ravens at the "Slab Rock" site, where Gyrfalcons nested in 1952 and 1959, also in stick nests. 21 June 1969.

1967, 1968, and 1969. Ravens may be at a disadvantage in years when Gyrfalcons occupy most of the cliffs with suitable nesting sites for these two species because the falcons occasionally take over active Raven nests; but it is difficult to estimate the degree of significance attached to this sort of molestation because Ravens are such uncommon nesters in any event. Also, we know from our 1967 observations at Cliff 54 that Ravens and Gyrfalcons can nest in close juxtaposition on the same cliff. In any case, any deleterious effect that this relationship may have on Ravens in good Gyrfalcon years is almost certainly offset by the more favorable opportunities afforded to Ravens in years when Gyrfalcons do not breed in large numbers. We have no indication that the occupancy of cliffs by Rough-legged Hawks influences in any way their occupancy by falcons or Ravens. Falcons sometimes force Rough-legs to move their nests, but only when the distances involved are under 50 yards or so. In the great majority of cases a pair of falcons and a pair of buteos can both occupy the same cliff with little friction between them. Peregrines and Ravens do not get along well together, and when Peregrines settle to breed on the same cliff with a pair of Ravens, the position of the Raven's nest may well determine their choice of nest site. In some cases this could force the Peregrines into a marginal or submarginal site. The same thing also applies in the case where Peregrines settle on the same cliff with Gyrfalcons. Thus, although some subtle forms of competition may exist among these cliff-nesters, the long term spatial and temporal effects on their populations are difficult to see, if indeed there are any.

Intraspecific territorial aggression is undoubtedly important in determining the overall density of these cliff-nesting species. On long, continuous stretches of cliff, as on the lower Colville, distances of less than half a mile between adjacent pairs of the same species are exceptional, although Peregrines and Rough-legged Hawks sometimes nest as close as one-quarter mile from conspecific pairs. Irving (1960) also reported the same for the Gyrfalcon on the upper Killik. Two miles is the closest we found them on the main

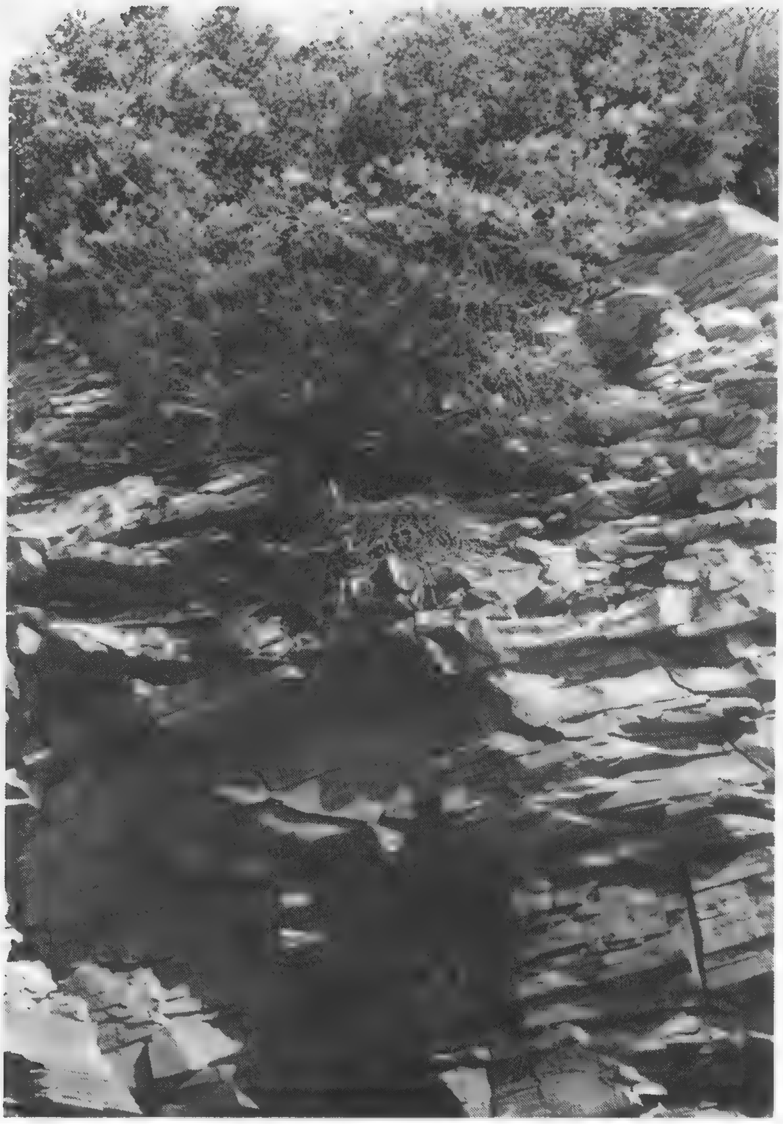


Figure 20. Raven's nest under overhanging projection of rock with willow. Such a nest may be used by Gyrfalcons in a future year. 25 June 1969.

Colville. This territoriality is manifested mainly in connection with the nesting site and does not include a defended feeding area. This means that most of the shorter cliffs accommodate only one pair of each species at most. We know of occupation by two or more pairs of the same species for only 19 of the 80 cliffs listed in Table 2; the shortest of these cliffs, 0.3 mile, had two pairs of Rough-legs, but all the other cliffs were longer than one mile.

The relative availability of their special food, ptarmigan, is a prime factor regulating the distribution and density of breeding Gyrfalcons. Whenever and wherever ptarmigan are scarce on the Arctic Slope, Gyrfalcons do not breed; in the past, the number of breeding pairs fluctuated by an order of magnitude from low to high years. Nevertheless we know from our observations in 1967, 1968, and 1969 that it is not necessary for the Gyrfalcons to have a huntable population of ptarmigan around the nesting sites. The density of Rough-legged Hawks also fluctuates, in response to changes in the numbers of microtine rodents; but since microtines along the Colville do not undergo the pronounced "cycles" characteristic of coastal populations of *Lemmus* and since the hawks can also exploit alternate forms of prey to some extent, the fluctuations of their populations are less extreme than those of the Gyrfalcons. We have no evidence that the availability of food influences in any way the density of Peregrines or Ravens nesting in the Colville Valley.

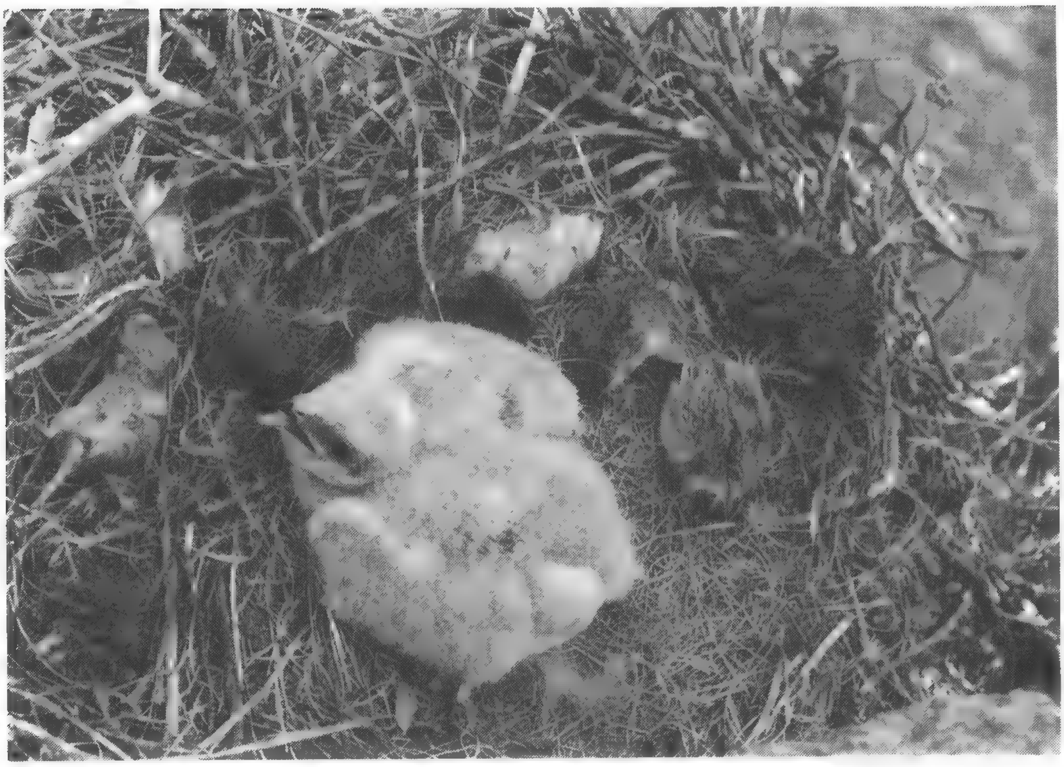


Figure 21. Downy Rough-leg surrounded in its nest by carcasses of collared lemming, red-back vole, and tundra vole. Note also chips of sphagnum and other bits of tundra greenery. 9 July 1967.

Unanswered Questions

We feel that there are still many important questions yet to be answered concerning these four species in arctic Alaska. Answers to these questions may provide more insight into many of the problems we have discussed. We are still left with an inadequate explanation of why Peregrines and Ravens, in particular, do not occupy more of the available nesting habitat. Perhaps the breeding pairs are self-limiting through some sort of social conventions or traditions that have become fixed on certain cliffs and not on others, as discussed by Wynne-Edwards (1962). Peregrines and Ravens are known to be highly site-specific in their nesting, and, even when reproduction exceeds the recruitment needed to maintain established pairs, and the population adds surplus adults, it may still be difficult for new pairs to colonize because social requirements of the species place such a high premium on the previous experience in breeding by at least one member of the pair (see Cade, 1960, for some further discussion). Obviously some new pairs must colonize, but the rate of establishment in a new territory may be very slow for species like the Peregrine and the Raven. Unlike the cases of the Gyrfalcon and Rough-legged Hawk, we have added very few newly occupied cliffs to the list of those known to have been in use by Peregrines along the Colville in 1952.

We need to know more about how much "normal" variability in breeding density and reproductivity exists in these arctic Peregrine populations from year to year and what factors are responsible for it. Has there been a permanent increase in numbers of Gyrfalcons along the Colville in recent years; or when feeding conditions are again severe, will the population return to the low numbers of previous years like 1958? The Gyrfalcon-ptarmigan relationship needs better quantification in terms of annual variations in distribution and numbers of ptarmigan populations. In particular, we need to know how far Gyrfalcons can travel from their aeries to exploit a local concentration of ptarmigan. Our findings in 1967, 1968, and 1969 suggest that it must exceed 10 miles. We need information on the early phases of the breeding cycle, especially with reference to how pairs become attached to particular cliffs and what the local food supply is like when the ground is still covered with snow.

We need details on the social organization and foraging behavior of Ravens in winter, and to learn how these details relate to the early phases of pair-formation and nest-site selection. We need much more information on feeding behavior and types of food eaten through the year. Why is the Raven such a rare breeder in northern Alaska when it is otherwise so resourceful and successful as a resident arctic species?

We need more information on the influence of microtine numbers on the breeding density and reproductive success of Rough-legged Hawks. In particular, we need to know more about their use of alternate prey, such as ptarmigan and ground squirrels, in years when microtines are low and how effectively they use these alternate prey species.

Conclusion

We have described the breeding season ecology of four avian predators as it has existed up to this time in essentially undisturbed wilderness environment, where few men have penetrated. All this is changing very rapidly now, and we fear that the Colville scenes, so familiar to us over the past 20 years, will quickly pass into oblivion with the coming of oil and "progress" in northern Alaska. The Colville Peregrines are already severely burdened with high levels of DDT residues (Cade, *et al.,* 1971); they produce thin-shelled eggs like those that have characterized the devastated populations of Britain, the eastern United States, and California (Ratcliffe, 1967; Hickey and Anderson, 1968); and, in 1969 and 1970 (Cade and Fyfe, 1970), they experienced the poorest reproductive output recorded since 1952. How much longer this fine species will be a part of the avifauna of the Arctic Slope is a moot question.

Once such a predator has disappeared from an ecosystem, changes in other populations are almost certain to follow. Perhaps the Northern Shrike (*Lanius excubitor*) will increase in numbers — there is some evidence that it already has — and will take over as the chief avian predator of the willow-inhabiting passerine birds (see Cade, 1967). The Gyrfalcon should hold its own and continue to thrive — perhaps it will even increase in numbers and broaden its ecological niche in the absence of Peregrines — unless the oil enterprise opens up the way for excessive human trafficking in this prized species for falconry and pet-keeping (Cade, 1968). The resourceful Raven will make out and even use the abandoned oil derricks for its home. The Rough-legged Hawk should also hold its own, except where drilling sites, radio stations, roads, pipelines, and other installations destroy its nesting habitat.

There is no consolation for the probable extinction of a bird like the Peregrine or for the destruction of a wilderness. The knowledge that some species — even some raptors — manage to persist in the face of man's massive onslaughts against the natural environment is small comfort, not enough to relieve us of a responsibility to speak against all forms of ecological madness.

Acknowledgments

Grants from the Arctic Institute of North America under contractual arrangements with the Office of Naval Research supported our field work. The Naval Arctic Research Laboratory, Barrow, Alaska, provided field transport and logistics. At a time when the "military establishment" is being harassed on all sides, we feel compelled to make a special public statement of our deep appreciation for the Department of the Navy's interest in supporting *basic* biological studies in northern Alaska during the past 25 years and for developing the finest arctic research station in the world, without which man's knowledge of the American Arctic would still be minuscule.

We thank Brian S. Cade, James H. Enderson, John R. Haugh, Walter R. Spofford, and Stanley A. Temple for valuable assistance in the field.

We also take this opportunity to commemorate Dr. Max C. Brewer for his 15 years of service (1956–1971) as Director of NARL and to wish him well in his new position as Alaska's first Commissioner of Environmental Conservation. His interest in work on Alaskan raptors has been second only to his love for Wolves and other carnivores, and much of what we know today about Peregrines and Gyrfalcons stems from his continuing concern for the welfare of these falcons.

ADDENDUM

In 1971, T. J. Cade, P. A. Spitzer, S. A. Temple, and J. W. Weaver again surveyed the entire 183-mile section of the Colville that we had studied in 1967–1969, as part of the IBP Tundra Biome study sponsored by the National Science Foundation. They made one boat trip during the incubation period in June and early July, and a second in late July and early August during the late nestling and fledging period.

A total of 25 pairs of Peregrines and five single adults occupied cliffs on the river. These falcons produced an estimated 57 eggs (54 actually observed); six pairs failed completely during egg-laying or early incubation; ten pairs failed during hatching or early in the nestling period; and the remaining nine pairs produced 14 young, or an average of only 0.56 fledglings per starting pair. Eight downy young died in their nests, evidently from parental neglect, paralleling a similar high incidence of 10 dead young found in 1969. Thus, in 1971, we witnessed the lowest number of breeding pairs ever recorded, eleven fewer than the high of 36 pairs found in 1959, and the poorest reproductive output. Addled eggs and eggshell fragments from 12 nests had average shell thicknesses ranging from 0.350 to 0.200 mm with a mean of 0.248 mm, or an indicated change in shell thickness of 31 per cent below the pre-DDT average of 0.360 mm. The Colville Peregrines cannot long survive these drastic alterations in reproductive physiology and productivity of young.

By contrast, even though ptarmigan and microtine rodents were in low numbers throughout the Colville drainage in 1971, twelve pairs of Gyrfalcons produced 18 fledged young, and 74 pairs of Rough-legged Hawks produced an estimated 107 young (96 actually observed from 70 nests).

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SOCIAL BEHAVIOR AND TAXONOMIC RELATIONSHIPS OF THE STORKS

M. PHILIP KAHL
Photographs by the author

The members of the stork family (Ciconiidae) are widely distributed throughout the world. Tropical Africa and tropical Asia hold the largest numbers of populations with as many as five species sometimes breeding in the same area — for example, in western Kenya.

Peters (1931) classified the 17 species of storks in 11 genera and two subfamilies. This and other phylogenetic studies of the storks, made when little was known of most species in life and under natural conditions, based their arrangements on characters of form and structure, or morphology. My studies (1959–1969), which encompassed wild populations of all 17 storks during their breeding seasons, revealed a number of behavioral and ecological traits bearing on taxonomic relationships within the family.

Study Areas and Methods

My field studies in North and South America, Africa, Asia, and Europe, as shown in Table 1, covered an 11-year period. In addition to observing wild birds under natural conditions, I studied, for various periods, the nestlings of the American Wood Stork, Yellow-billed Stork, African Openbill Stork, and Marabou Stork, hatched and hand-reared in captivity.

I observed the wild birds principally with 7× binoculars and a 15–30–60× telescope from elevated towers or tree-platforms erected within five to 20 meters of active nests. In the field, I generally dictated descriptions of behavioral sequences into a portable tape recorder and later transcribed them, and supplemented my observations by 16 millimeter motion-pictures and 35 mm still photographs, which I later analyzed to confirm details and to quantify certain aspects of the behavior patterns.

In the following treatment I have attempted to give a general picture of the most characteristic behavioral traits of each species and to use these—in conjunction with other characters—to assess taxonomic relationships within the family.

For a more detailed treatment of the behavior of the Ciconiidae than is possible here, the reader is referred to Schüz (1942) and Kahl (1966, in press, a, b, c, d, and others in preparation).

In the main portion of this paper, I have used the scientific nomenclature of Peters (1931). Under the "Discussion" I suggest some changes in nomenclature and sequence, based on my new evidence.

Stork Courtship: A General Picture

All storks show the greatest number of ritualized social displays during the period of pair-formation and courtship. Many such displays are species-specific and presumably largely genetically determined. Certain ones appear to be as valuable in assessing relationships and differences between species and genera as are morphological characters.

At the start of the breeding season the males of all storks typically establish themselves on a potential nest site, which may be a nest used in a previous season or merely a site where they can build a new nest. Once a male has taken possession of a nest site, he behaves aggressively to all other storks — regardless of sex — that come near. Other males generally avoid an established male, or else they fight, either replacing him or being driven off by him. Reproductively "ripe" females, however, repeatedly attempt to approach an established male on a nest site. Such females make no attempt to fight with the male, although he frequently attacks and drives them away. Even after a violent attack by a male, the female merely retreats and then, eventually, returns and approaches the male once again. In repeated approaches, the male attacks the female less vehemently. He eventually accepts her and allows her to enter the nest site with him. Once a male accepts a female, copulations and nest-building follow.

During the period when the male alone defends the nest site against all other storks and the female attempts to join him, both give frequent and diverse ritualized social displays. Such displays apparently serve as signals to the companion bird and help to coordinate the activities of pair-formation by reducing aggression between potential mates. Many of these social displays disappear rather quickly once pair-formation is accomplished. Some, however, such as the Up-Down "greeting" display, described below, may persist throughout the breeding season.

In the following presentation, I have described certain displays as being most characteristic of one particular sex. However, I have seen practically all of these social displays, at least occasionally, in the sex other than the one in which they are most typical.

The Wood Storks

(Plates I and II)

The four species of wood storks, sometimes inappropriately called "wood-ibises," live throughout many of the tropical regions in the Old and New World. The American Wood Stork (*Mycteria americana*) inhabits the Americas, from Florida southward to central Argentina; the Yellow-billed Stork (*Ibis ibis*) ranges throughout most of tropical Africa; the Painted Stork (*I. leucocephalus*) is widely distributed from West Pakistan and India to Indochina; and the Milky Stork (*I. cinereus*) occurs locally from Cambodia and Vietnam to Sumatra and Java. The species of wood storks are allopatric — i.e., they live in different areas — except for the overlap in Indochina of the ranges of the Painted Stork and Milky Stork.

Social Displays. — The four wood storks are remarkably alike in behavior; as a group, they possess several distinctive social displays that set them apart from the other storks (Kahl, in press, b).

Lone males on nest sites typically show bouts of Display Preening when courting females approach them. In this display, the male "pretends" to strip down the feathers of a partially open wing (Plate IIb), although his bill often does not actually touch the feather that he appears to be preening. The movements of Display Preening often continue with a clock-like rhythm for several minutes, with the displaying male alternately switching his attention back and forth from one wing to the other and preening either in front of, or behind, the wing. Display Preening appears in a similar form in all three of

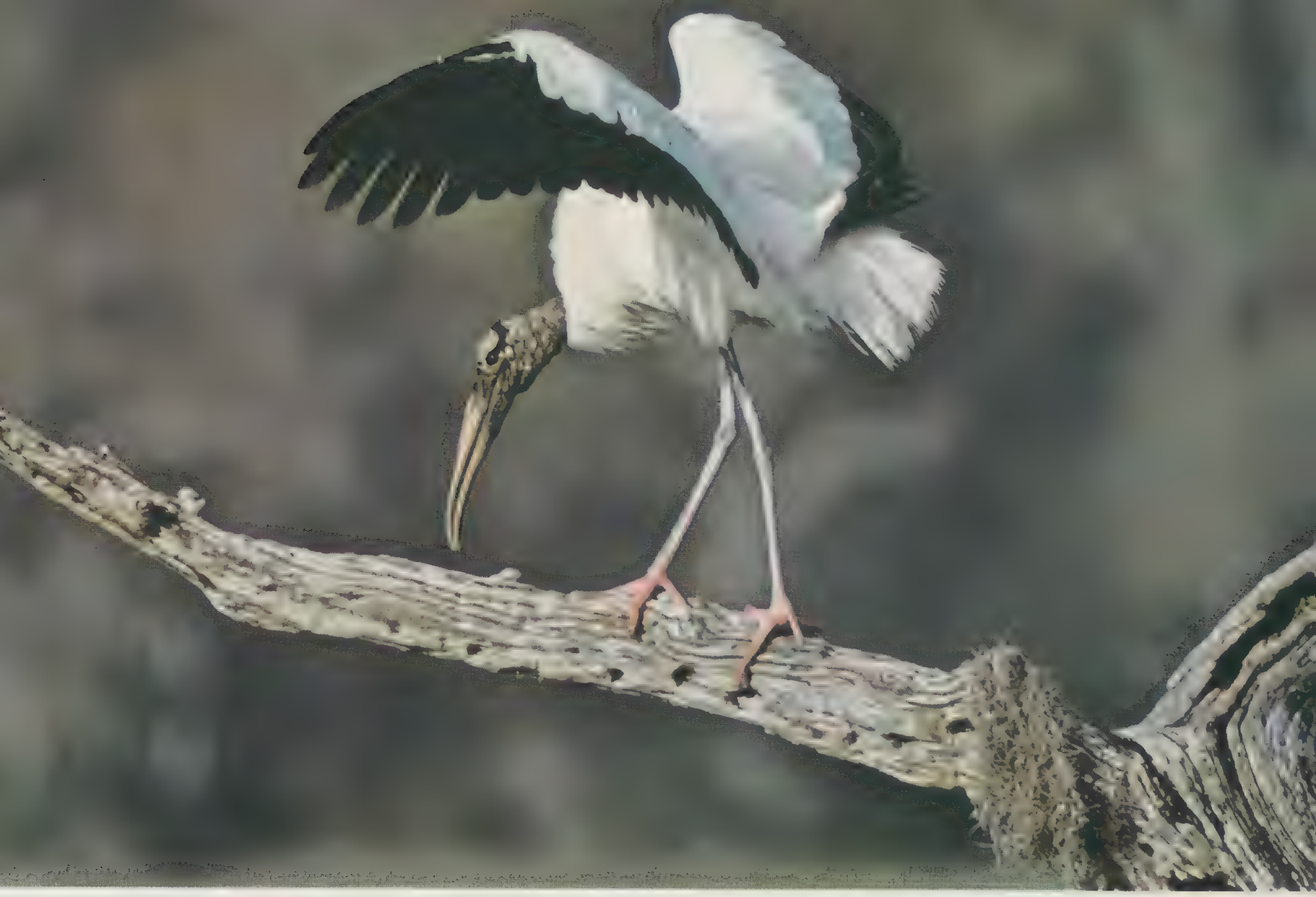
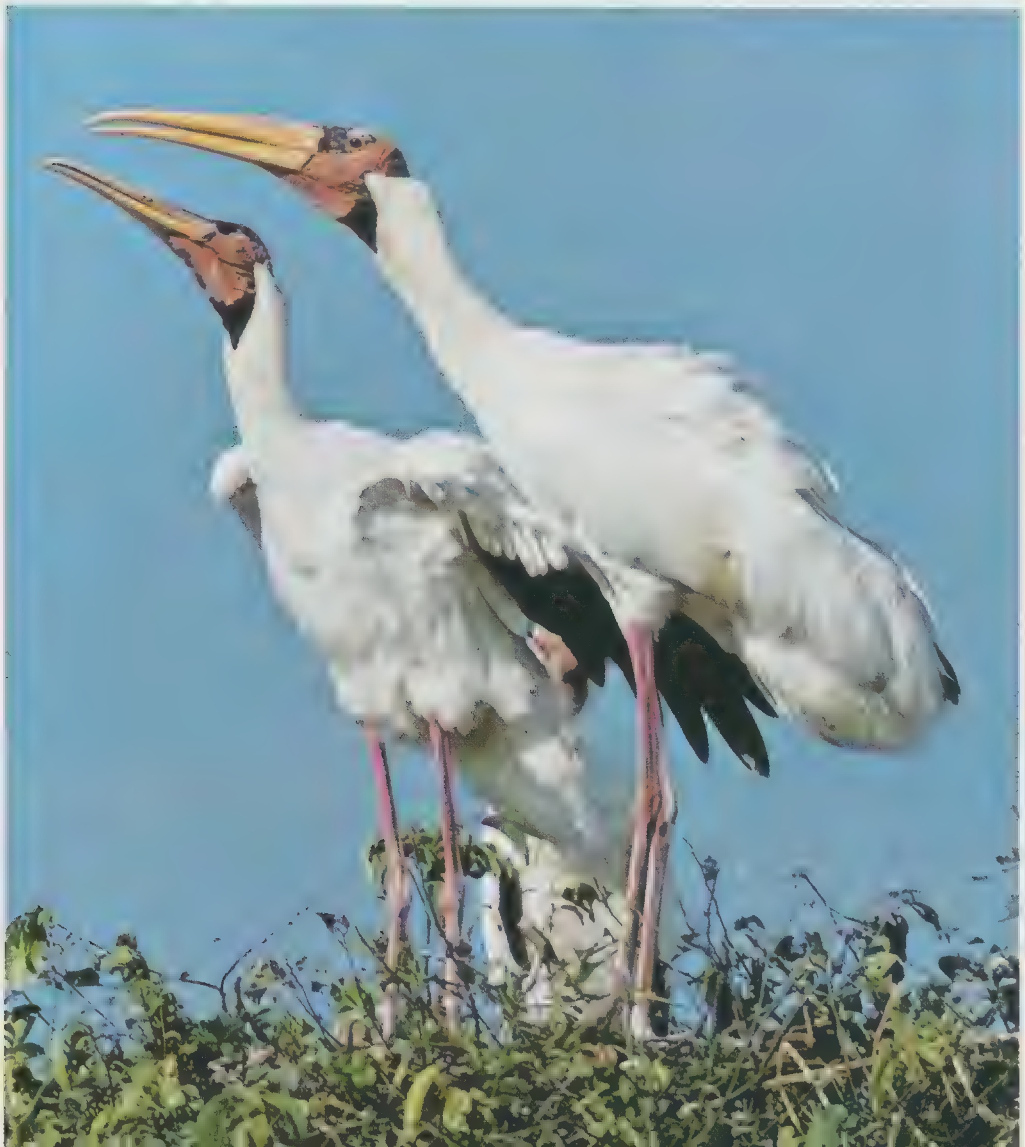


Plate I. American Wood Stork, *Mycteria americana;* Corkscrew, Florida. Adult in Balancing Posture near a courting group *(above)*.

Milky Stork, *Mycteria* [=*Ibis*] *cinerea;* Pulau Dua, Java, Indonesia. Pair performing a mutual Up-Down display; male on right *(below)*.



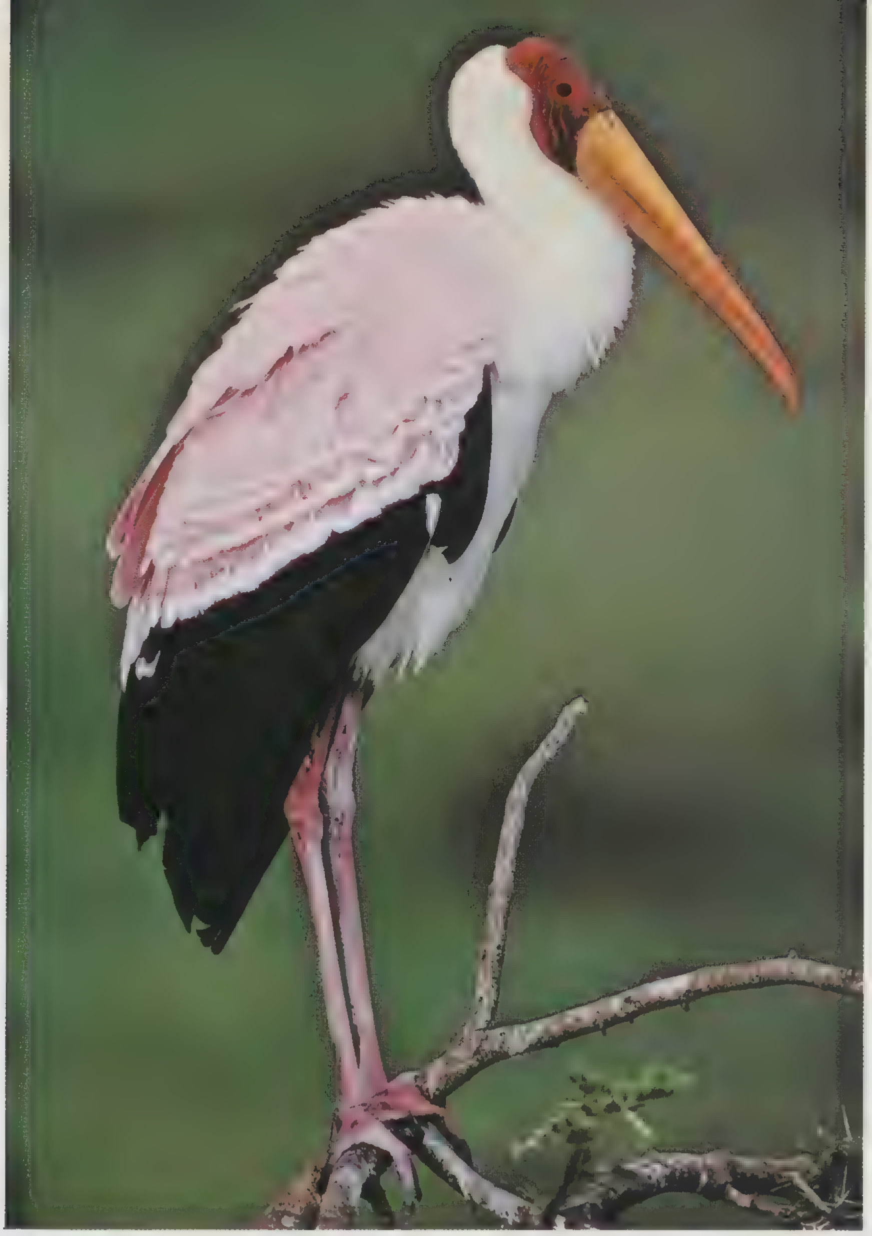


Plate II.
Yellow-billed Stork,
Mycteria [=*Ibis*] *ibis;*
Kisumu, Kenya.
Adult in full breeding
plumage, with head-skin
partially retracted *(left)*.

Painted Stork, *Mycteria*
[=*Ibis*] *leucocephala;*
Bharatpur, Rajasthan,
India. Courting pair:
male in front performing
Display Preening behind
the wing; female in
background, Gaping *(right)*.

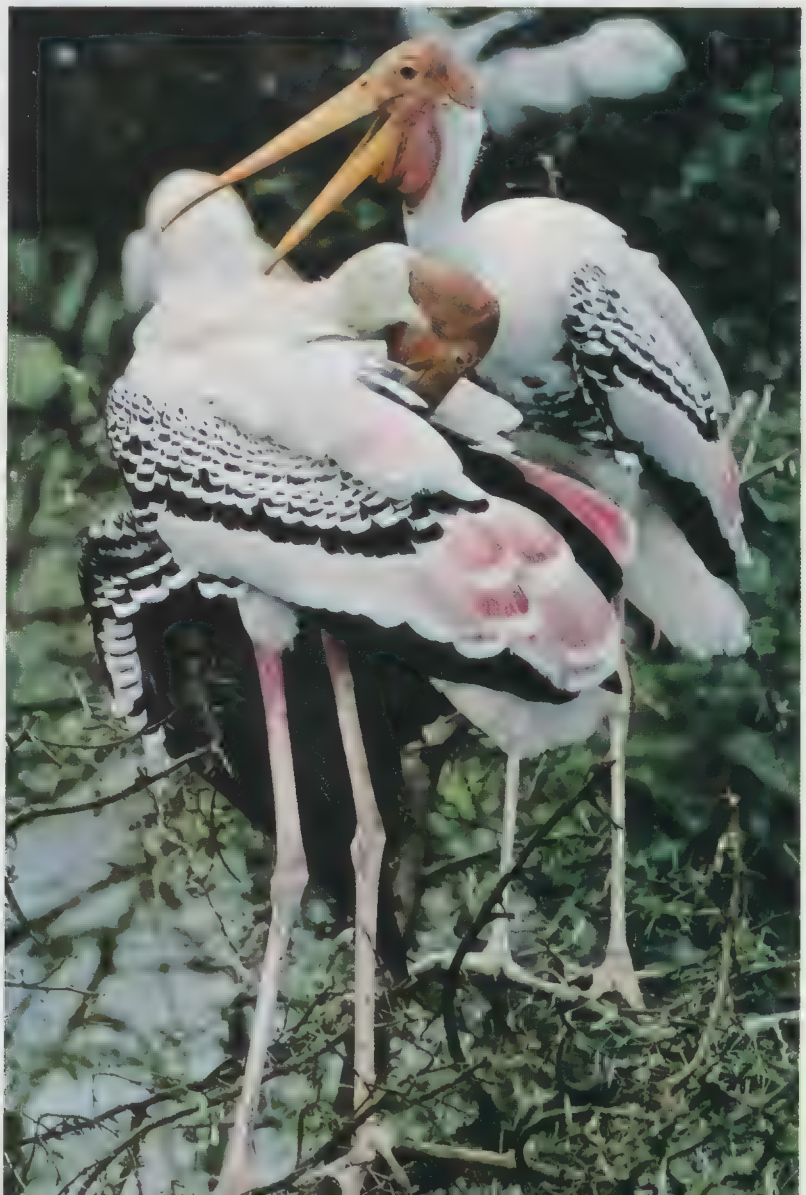


TABLE 1

Principal Dates and Study Areas for Each Species of Stork*

Species	*Major study areas*	*Dates*
American Wood Stork (*Mycteria americana*)	Florida, U.S.A.	1959–1963; 1968–1969
Yellow-billed Stork (*Ibis ibis*)	Kisumu, Kenya	1964–1967
Painted Stork (*Ibis leucocephalus*)	Bharatpur, Rajasthan, India	August–October 1966 August–October 1967
Milky Stork (*Ibis cinereus*)	Pulau Dua, Java, Indonesia Grand Lac, Cambodia	March 1968 April 1968
Asian Openbill Stork (*Anastomus oscitans*)	Bharatpur, Rajasthan, India Bharatpur, Rajasthan, India Wat Pai Lorm, Thailand	August–October 1966 August–October 1967 February 1968
African Openbill Stork (*Anastomus lamelligerus*)	Kisumu, Kenya Queen Elizabeth Park, Uganda	1963–1967
Abdim's Stork (*Sphenorhynchus abdimii*)	Busia, Kenya Busia, Kenya Lake Shala, Ethiopia	January–March 1964 January–March 1965 April 1967
Woolly-necked Stork (*Dissoura episcopus*)	Hoima, Uganda; Kilifi, Kenya Bharatpur, Rajasthan, India Periyar, Kerala, India	1964–1967 August–October 1967 December 1967
White Stork (*Ciconia ciconia*)	Milicz, Poland	March–May 1969
Black Stork (*Ciconia nigra*)	Natal, South Africa Milicz, Poland	October 1964 March–May 1969
Maguari Stork (*Euxenura galeata*)	Corrientes Province, Argentina	August–September 1969
Black-necked Stork (*Xenorhynchus asiaticus*)	Bharatpur, Rajasthan, India	August–October 1966 August–October 1967
Saddlebill Stork (*Ephippiorhynchus senegalensis*)	Kisumu, Kenya; western Uganda	1964–1967
Jabiru Stork (*Jabiru mycteria*)	Corrientes Province, Argentina	August–September 1969
Greater Adjutant Stork (*Leptoptilos dubius*)	Kaziranga, Assam, India	December 1967
Marabou Stork (*Leptoptilos crumeniferus*)	Kitale, Kenya; western Uganda	1964–1967
Lesser Adjutant Stork (*Leptoptilos javanicus*)	Nowgong, Assam, India	November 1967

*Scientific nomenclature follows Peters (1931).

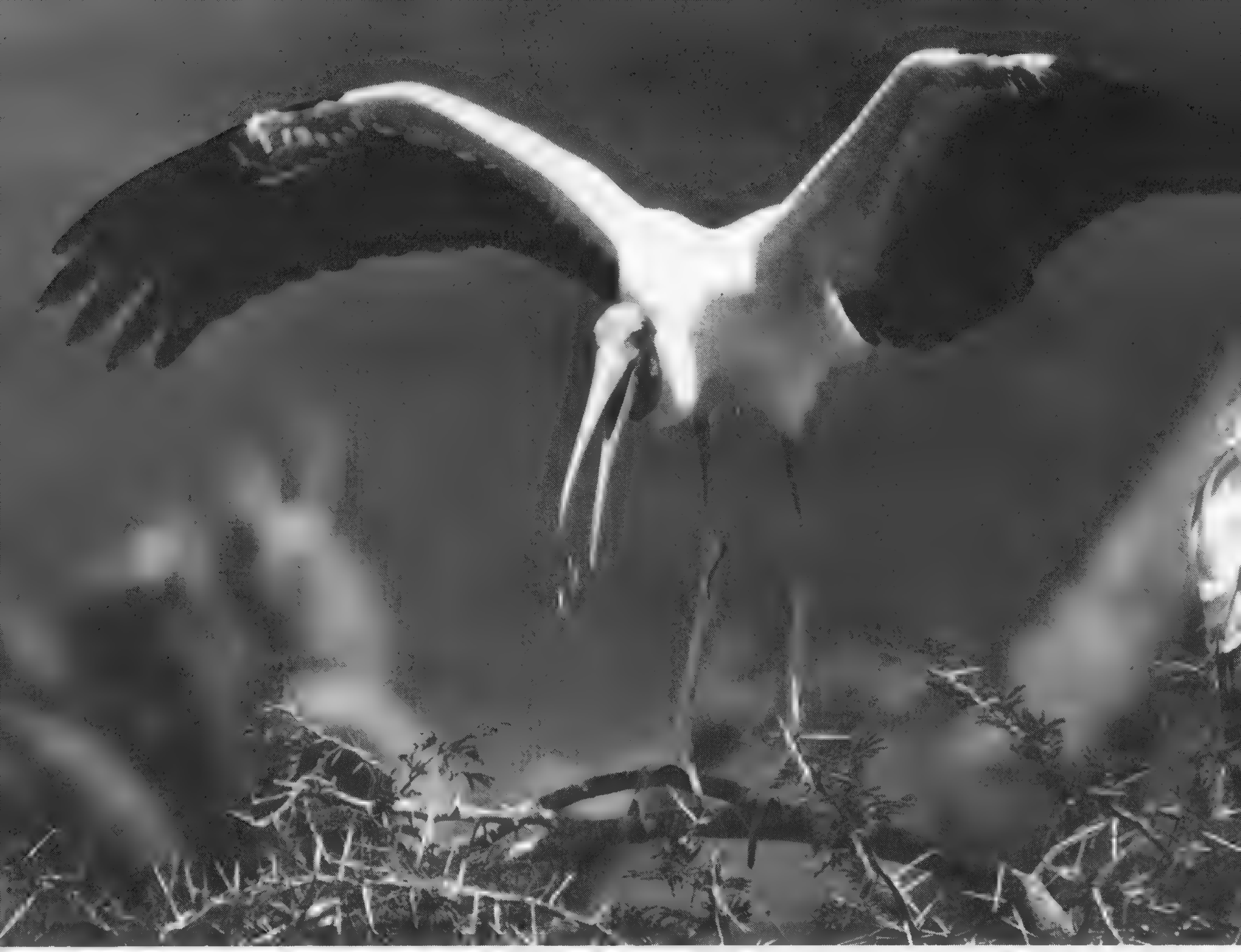


Figure 1. A female Yellow-billed Stork in the Balancing Posture, and Gaping, approaches an unmated male, on the extreme right, during pair-formation (Kisumu, Kenya, April 1966).

the Old World species. In the American Wood Stork it differs slightly in that the bird moves the bill somewhat less, and the wing more, during the apparent preening movement, drawing the feathers past the bill with a lifting motion of the nearly closed wing.

Meanwhile, the approaching female adopts a Balancing Posture, with wings held widely spread and bill open in the Gaping display (Figure 1). She often maintains these displays for 30 seconds or more after landing near a male, or walking toward him along a nearby branch. Eventually, the female closes her wings but often continues Gaping for long periods, even after she has entered the nest site and is standing alongside the male (Plate IIb). Gaping closely resembles thermoregulatory panting, from which it may be derived, but it occurs even when the bird is not overheated and it is not accompanied by an increased breathing rate.

After a pair is formed, both members "greet" each other with mutual Up-Down displays whenever one mate returns to the nest after an absence. In the Up-Down, the bird throws its head and neck upward so that the bill is nearly vertical (Plate Ib), gapes the bill widely, and then lowers its head and neck and swings them slowly from side to side (Figure 2). As the head is lowered, the bird utters a series of hissing-screams or "fizzing" notes.

Although the Up-Down is similar in all four wood storks, there are noticeable quantitative differences. In the American Wood Stork, the bill usually remains open between vocalizations. In the Yellow-billed Stork, single, or occasionally double, snaps of the bill are interspersed at two- to three-second intervals between vocalizations. The Painted Stork gives double or triple snaps and quickens the tempo of the entire display so that the bill reaches the "down" position in approximately three to four seconds — about one-half the time taken by the other three species. Furthermore, the vocalizations of the Painted Stork are considerably weaker than those given by the other wood storks, being audible for only 20 to 30 meters, as opposed to 100 meters on windless days. The Milky Stork gives an Up-Down that is similar in tempo and vocalizations to the American Wood Stork and the Yellow-billed Stork, but multiple bill-snaps, three to five in a series, are usually given between vocalizations.

During copulation the male wood stork clatters his mandibles rapidly together and, at the same time, beats his bill roughly back and forth against the bill of the female. The female holds her wings widely spread during the display. This Copulation Clattering is similar in all four wood storks (Figure 3).

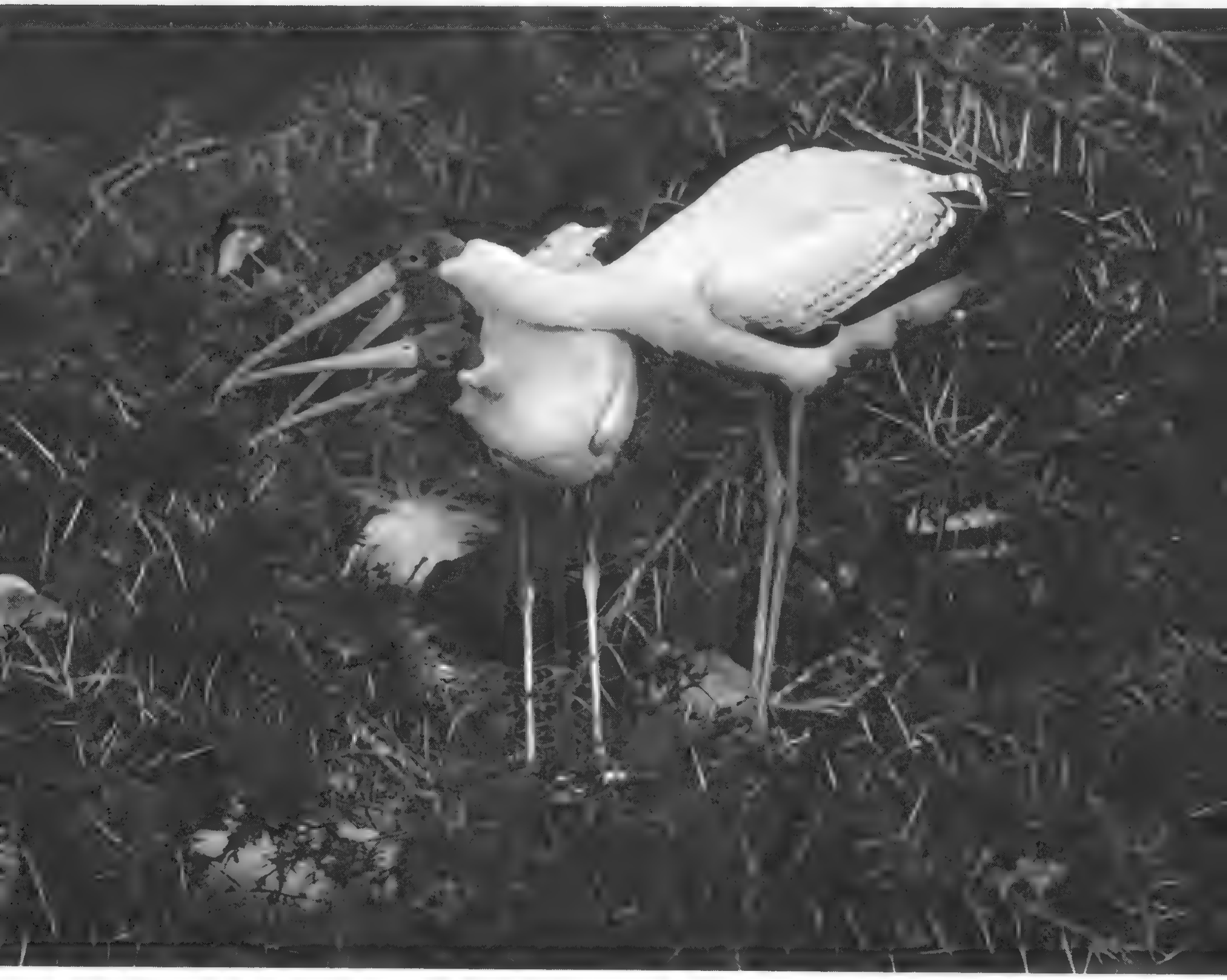


Figure 2. A pair of Yellow-billed Storks; the male on right performing an Up-Down immediately after he returned to the nest (Kisumu, Kenya, April 1966).

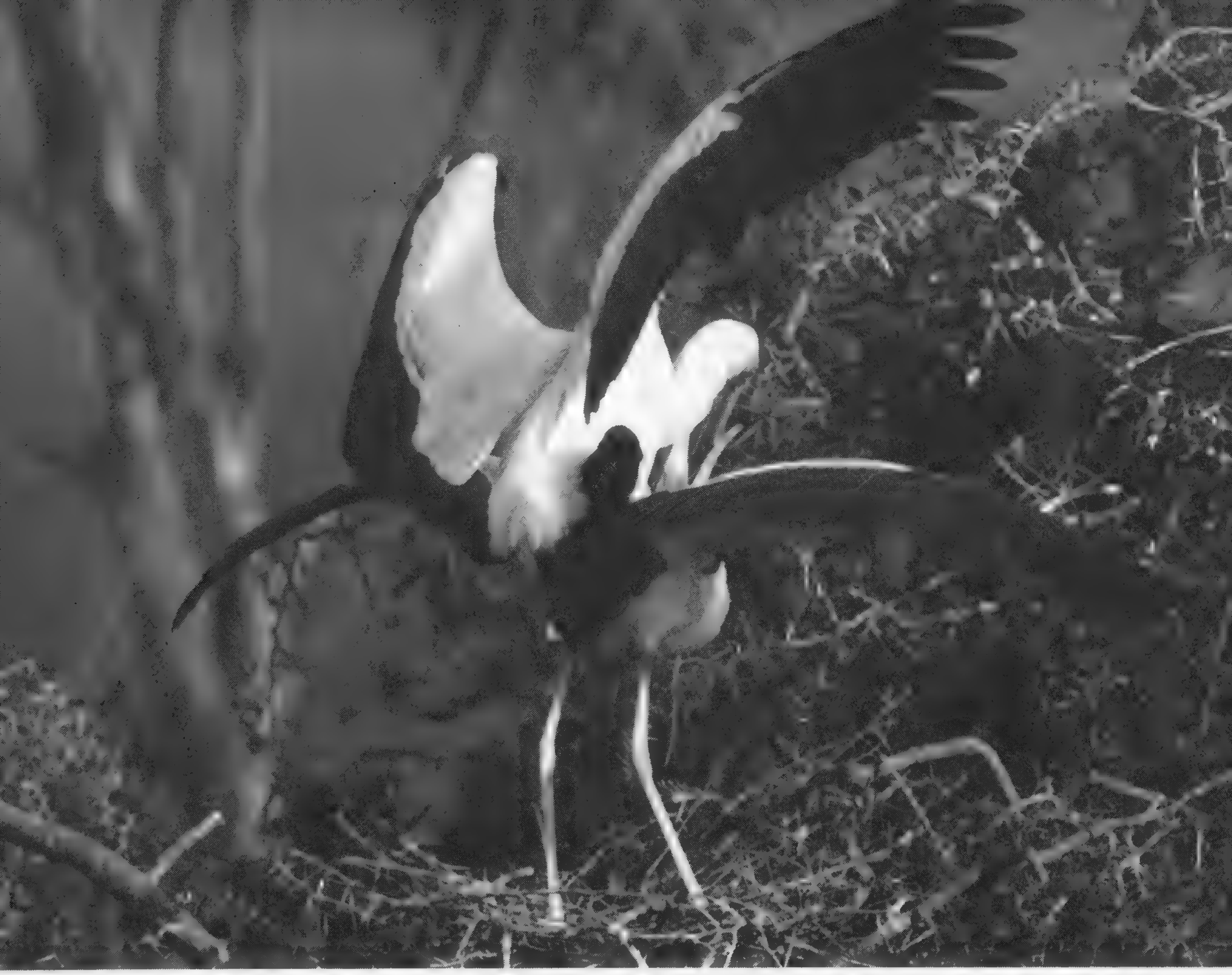


Figure 3. Copulation Clattering in Yellow-billed Storks, viewed from the rear (Kisumu, Kenya, April 1966).

Other Characteristics. — The wood storks are similar to each other in body proportions, general plumage pattern, and bill structure. They differ mainly in the amount of naked skin on the head and neck and in the color of the wing-coverts and other ornamental feathers, especially in the breeding season. Their similar bill structure reflects a corresponding feeding technique. They forage, mainly for small fish, by feeling in shallow water with a partially open bill, often stirring underwater vegetation with their feet and snapping shut on any item that comes in contact with their mandibles. Experiments with the American Wood Stork have shown that they are capable of efficiently capturing aquatic prey even when deprived of frontal vision (Kahl and Peacock, 1963; Kahl, 1964). Locating prey tactily enables wood storks to feed in turbid water or in dense vegetation, where visibility is poor, but such a feeding technique is effective only where the density of prey animals is relatively high.

The Openbill Storks
(Plate III)

The two species of openbills — the African Openbill Stork (*Anastomus lamelligerus*) and the Asian Openbill Stork (*A. oscitans*) — inhabit tropical regions of the Old World. Both are highly gregarious; they usually breed in large colonies, often in conjunction with other species of water birds.

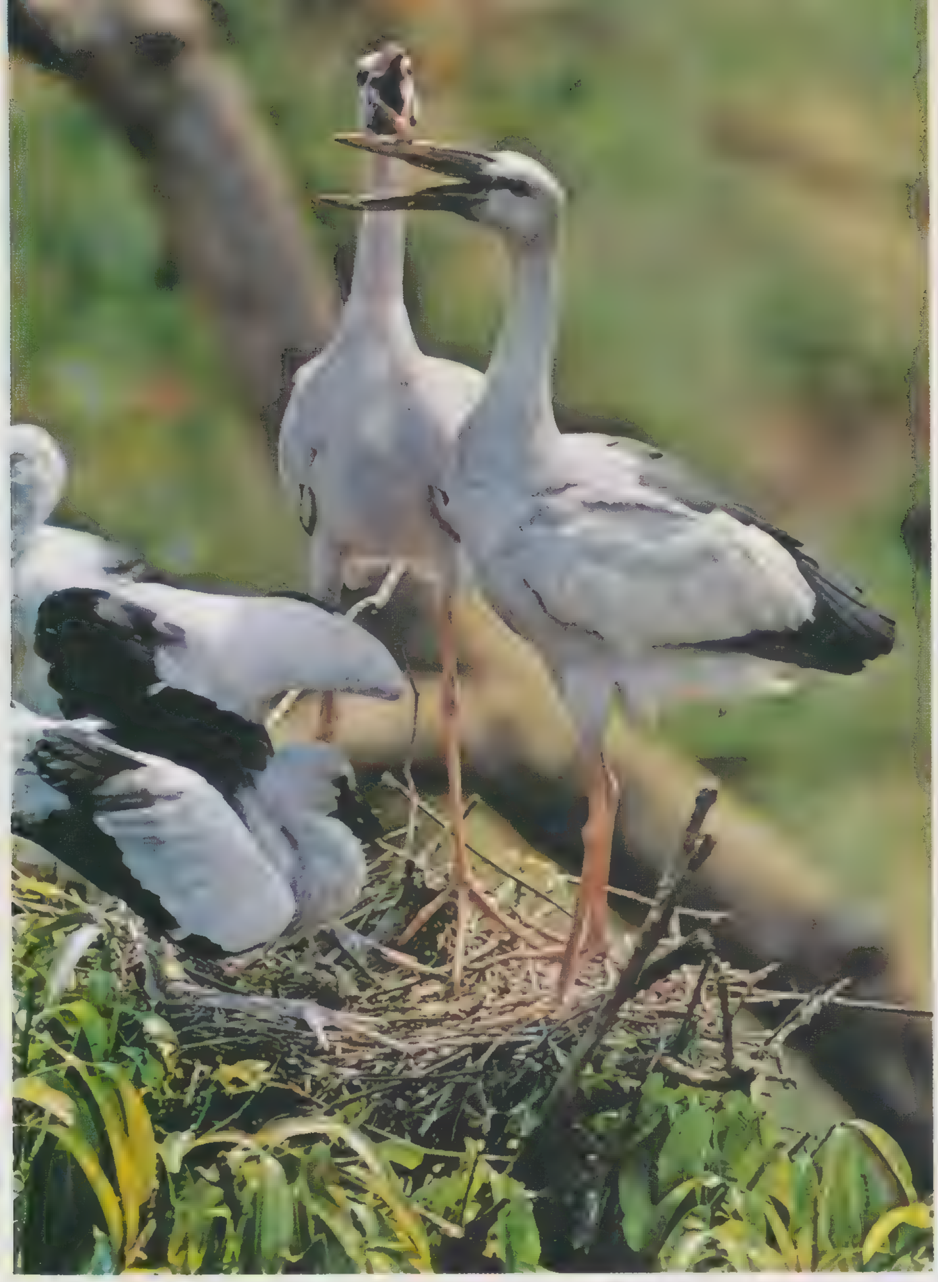
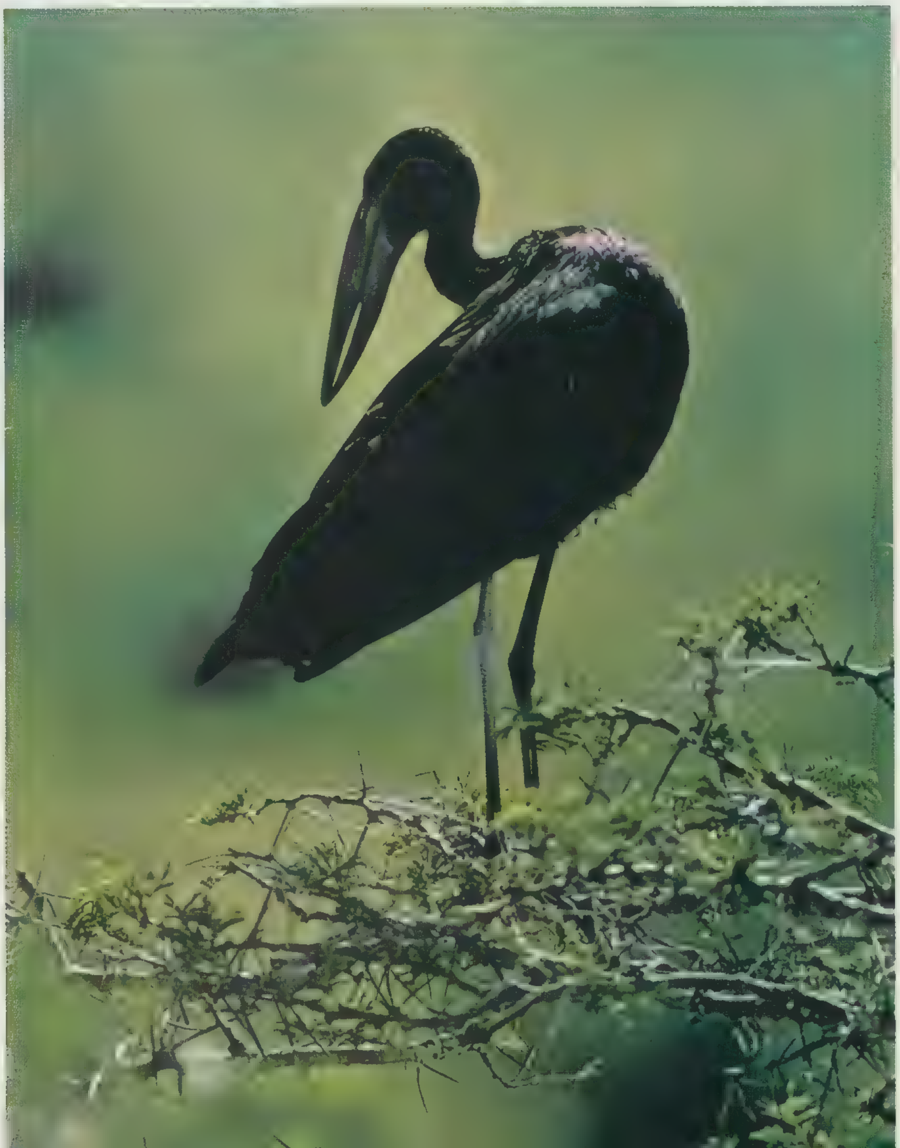


Plate III.
Asian Openbill Stork,
Anastomus oscitans;
Wat Pai Lorm, Thailand.
Pair performing a mutual
Up-Down display; female
on right; nestling, about
40 days old, begging *(left).*

African Openbill Stork,
Anastomus lamelligerus;
Kisumu, Kenya.
Adult preening, showing
gap in bill and curly
breeding plumes on breast
and abdomen *(right).*



Social Displays. — My observations indicate that the two species resemble each other closely in most aspects of behavior. However, my studies of breeding aggregations of the African species are not complete enough to permit precise comparisons with respect to all displays.

During courtship, male Asian Openbill Storks give a bizarre display, termed the Advertising Sway. An unmated male stands on a nest site, bends forward until its bill is pointed downward almost between its feet, and then

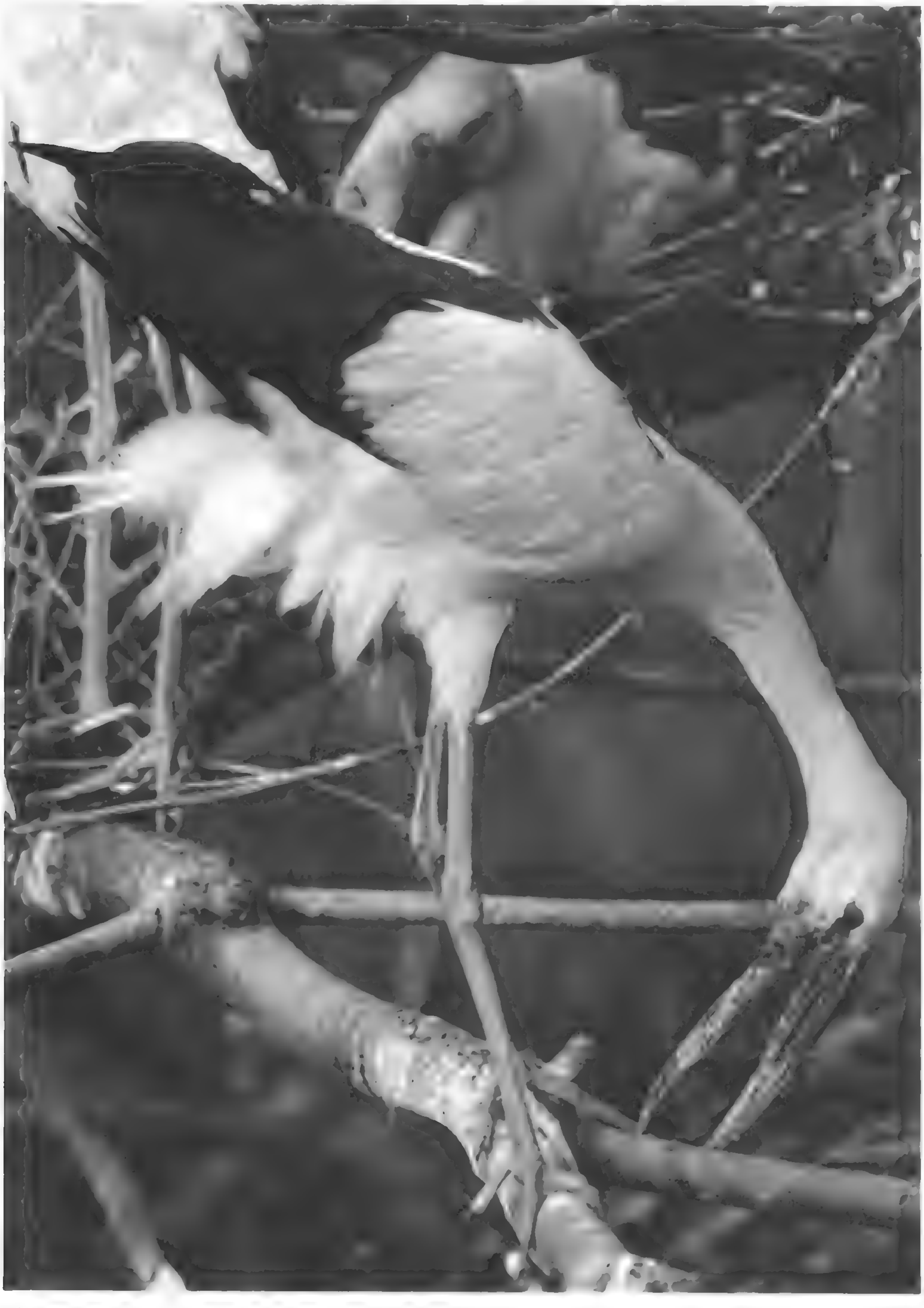


Figure 4. A courting male Asian Openbill Stork performing the Advertising Sway near a potential nest site in a breeding colony. Note the strongly spread of the undertail coverts and lifted wing-tips (Wat Pai Lorm, Thailand, February 1968).

stiffly shifts its weight back and forth from one leg to the other, lifting each foot slightly off the perch with each oscillation (Figure 4). This display appears to be a highly ritualized variant of the Swaying Twig-Grasping display observed in the Marabou, Greater Adjutant, and Lesser Adjutant Storks that comprise the genus *Leptoptilos* (described below; also see Kahl, 1966, and in press, a) and — in a more subtle form — in the wood storks (Kahl, in press, b). The Advertising Sway was not observed in the African Openbill, but I suspect that this was due to insufficient observation during the courtship period.

Once pairs are formed, both sexes give frequent Up-Downs. The birds strongly arch their necks upward and forward, gape their bills widely (Plate IIIa), and utter vocalizations at one- to two-second intervals as they move their heads and necks downward until their bills reach nearly to the substrate. In the Asian Openbill these vocalizations are a hollow, nasal, honking *huun, huun, huun.* In the African Openbill the homologous vocalizations have a higher-pitched and more rasping or croaking quality. The vocalizations of both species are rather loud and can be heard up to 100 meters on windless days.

During copulation both species of openbills produce a Copulation Clattering similar to that of the wood storks, but the clattering sound is made largely by the male's bill beating roughly back and forth against the bill of the female. During the copulation, the male openbill does not clatter his mandibles loudly together (Kahl, 1970; in press, d), as do male wood storks.

Other Characteristics. — Except for plumage color, the two openbills are quite similar. The African bird is predominantly black, with modified feather-tips of brown and dark iridescent green and purple on the wing-coverts, back, abdomen, and breast. The Asian bird is largely white, with black primaries, secondaries, scapulars, and tail. Both are similar in size, body proportions, and bill structure. The unique open bill that gives the birds their common and generic names apparently is related to their specialized diet, which consists mainly of shelled molluscs. For a discussion of the adaptiveness of the open bill in the feeding of these storks, consult Huxley (1960) and Kahl (1971b).

The "Typical" Storks

(Plates IV, V, and VIa)

The White Stork (*Ciconia ciconia*) of Eurasia is certainly the most widely known member of the family. Until recently it was the only stork that had been studied intensively at the nest (Siewert, 1932, 1955; Haverschmidt, 1949; Hornberger, 1967; and Schüz, 1942, 1943). It is still the only species that has been extensively banded and for which much information is available on longevity, dispersal, migration, orientation, etc.

Also included in this group are the Black Stork (*C. nigra*) of Eurasia and southern Africa; the Abdim's Stork (*Sphenorhynchus abdimii*) of the African tropics; the Woolly-necked Stork (*Dissoura episcopus*) of the African and Asian tropics; and the Maguari Stork (*Euxenura galeata*) of South America.

Social Displays. — The "typical" storks show a diversity of social displays (Kahl, in press, c). However, here we will consider only those displays shown by all five species that are most diagnostic of this group and that best elucidate the relationships between its members.

During pair-formation, and for several days thereafter, a male on the nest usually adopts the Head-Shaking Crouch when a female approaches. This

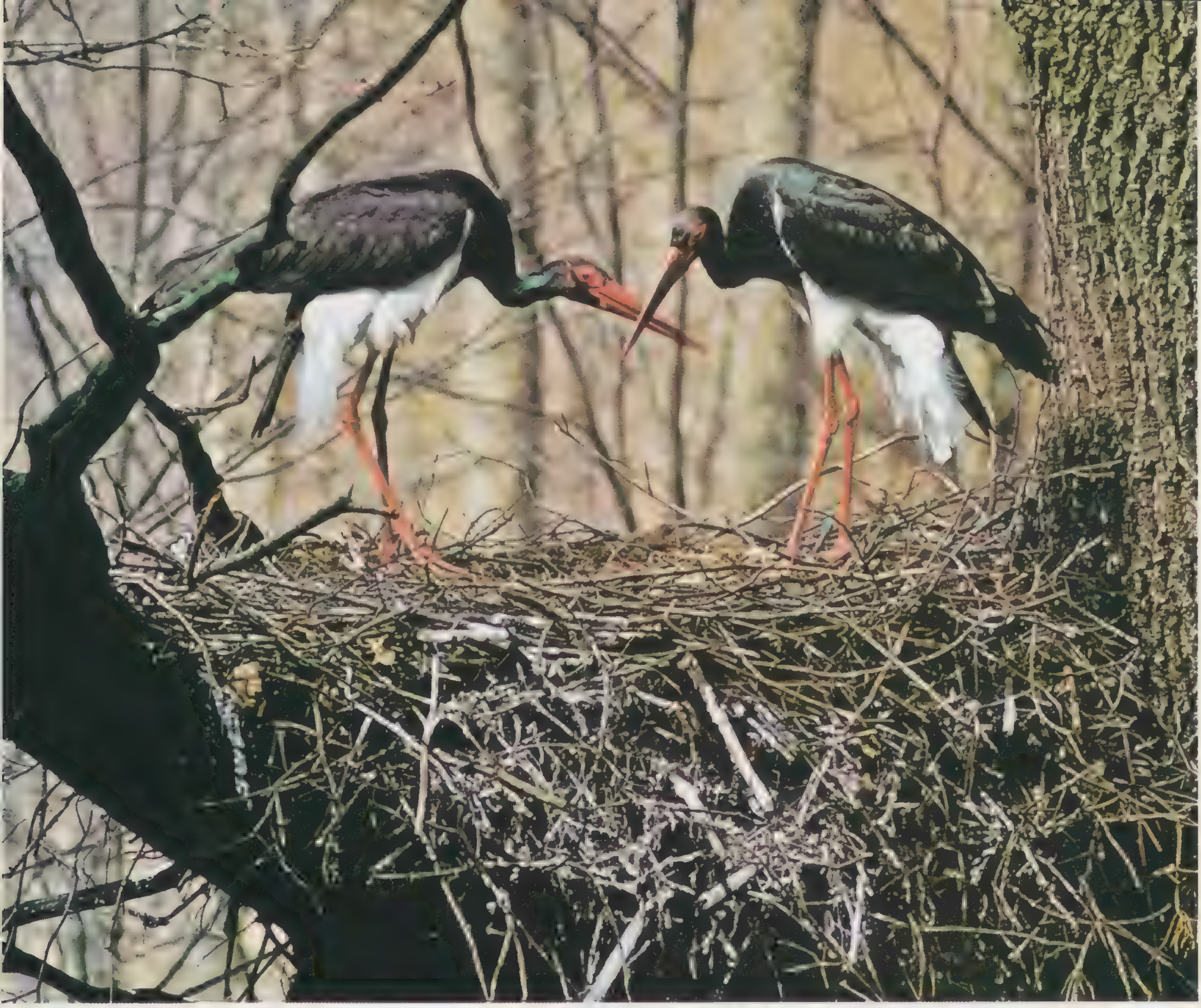
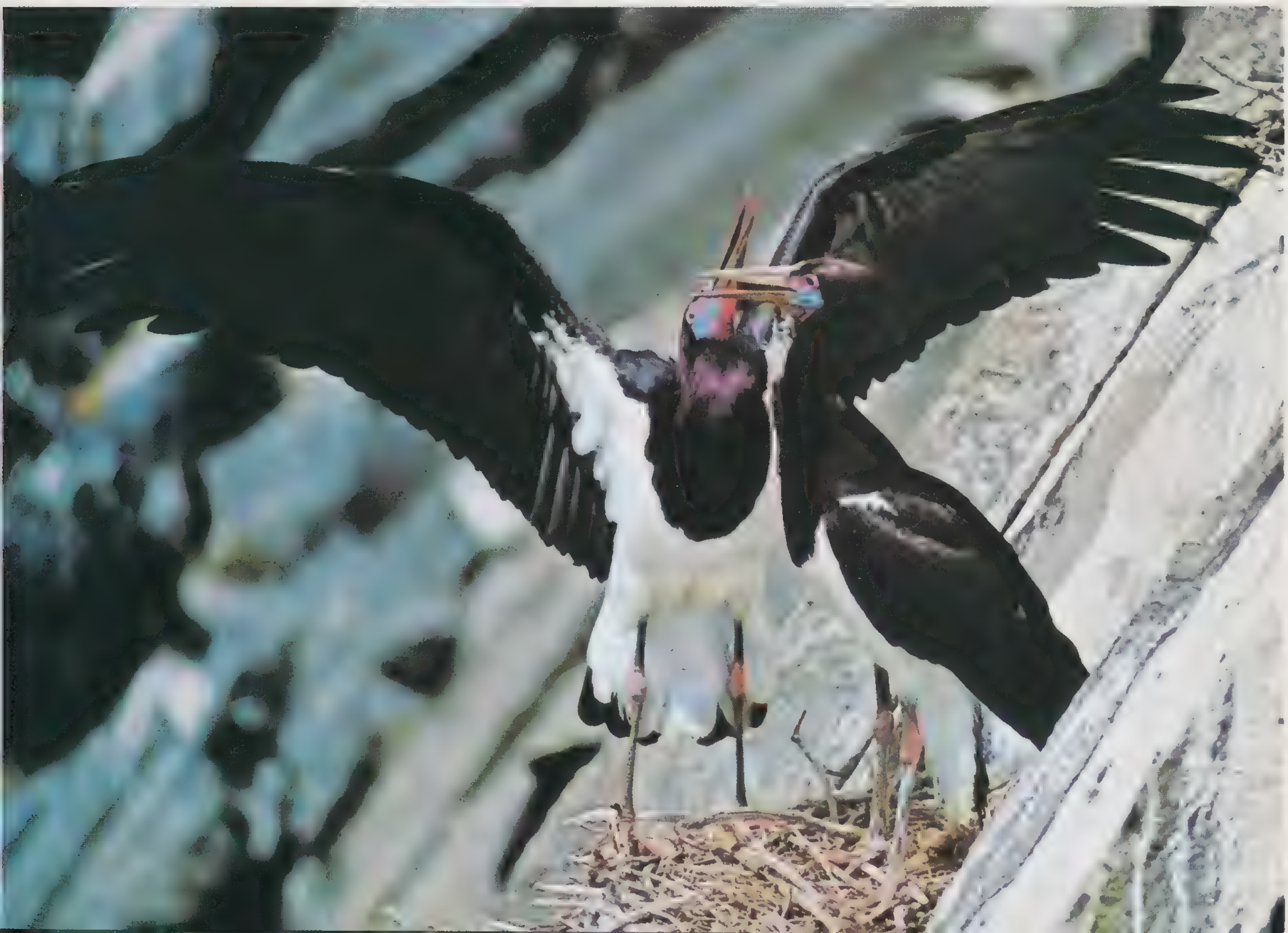
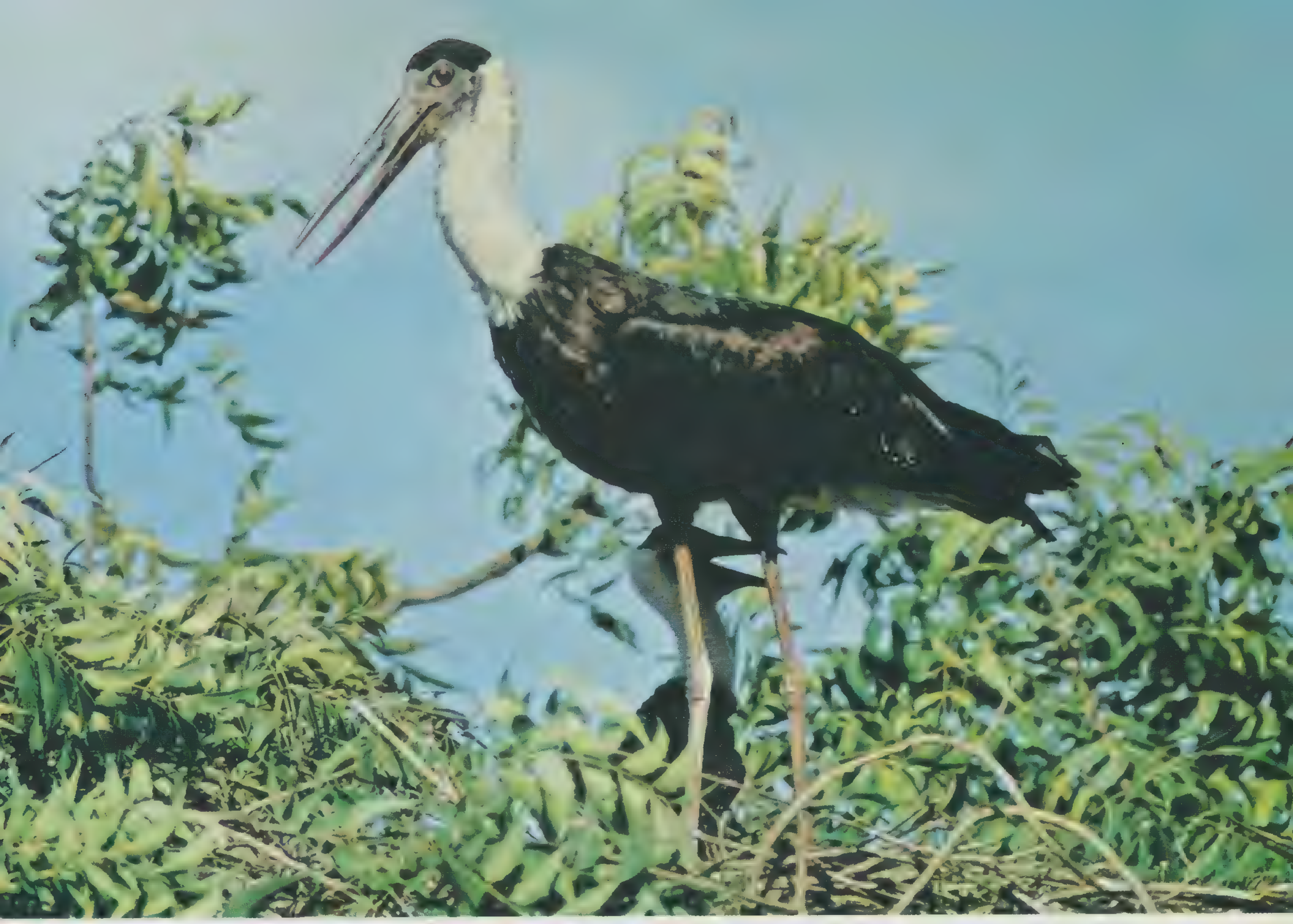


Plate IV. Black Stork, *Ciconia nigra;* Milicz, Poland.
Pair performing an Up-Down display; male on left *(above).*

Abdim's Stork, *Ciconia* [=*Sphenorhynchus*] *abdimii;* Lake Shala, Ethiopia.
Pair performing a mutual Up-Down display; male on left *(below).*





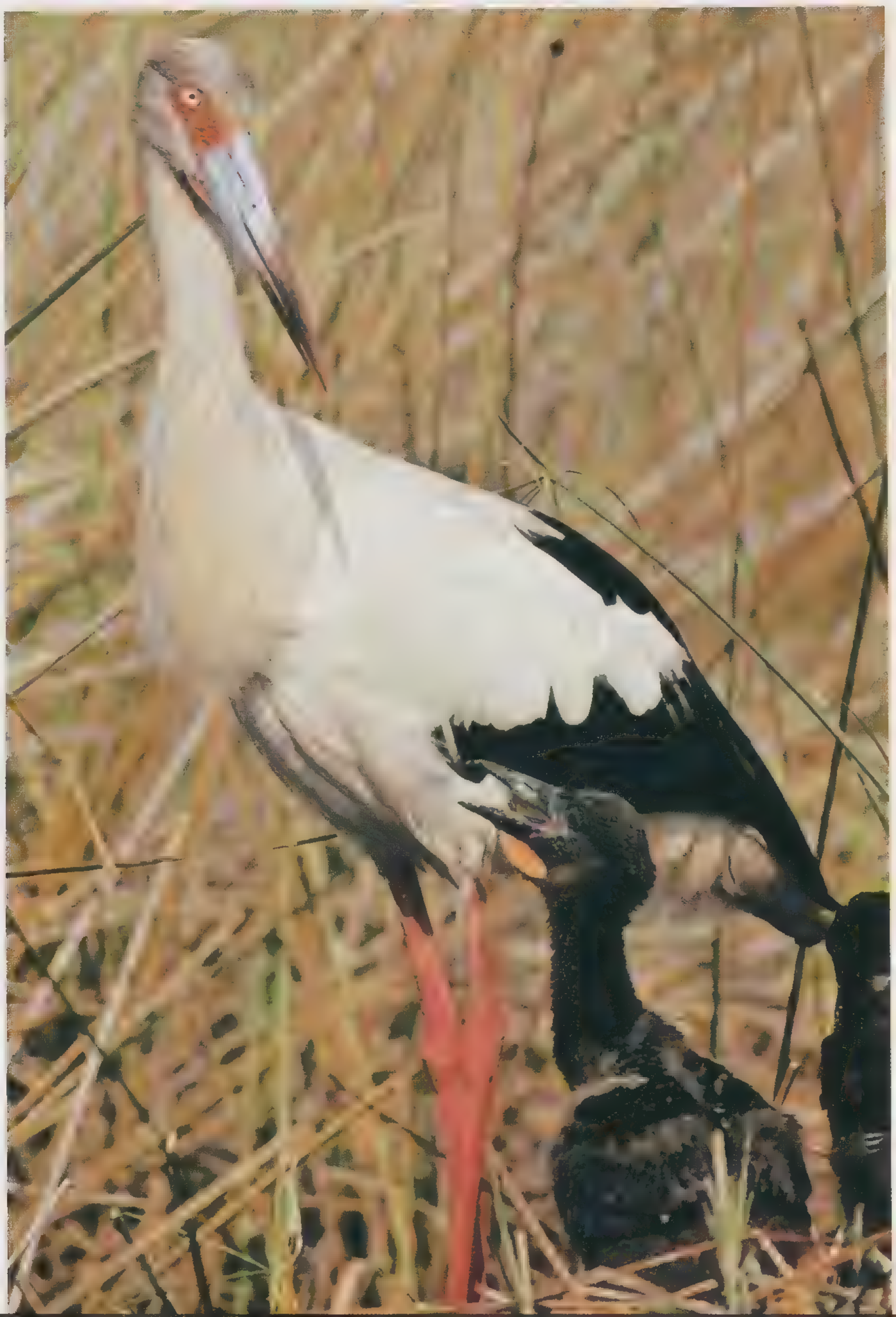


Plate V.
Woolly-necked Stork,
Ciconia [=*Dissoura*] *episcopus;*
Kiraoli, Uttar Pradesh, India.
Adult on nest, standing in alert
posture over nestling about
20 days old *(above).*

Maguari Stork,
Ciconia [=*Euxenura*] *maguari;*
Santa Teresa, Corrientes,
Argentina. Adult female
on nest with two nestlings
about 25 to 30 days old *(right).*

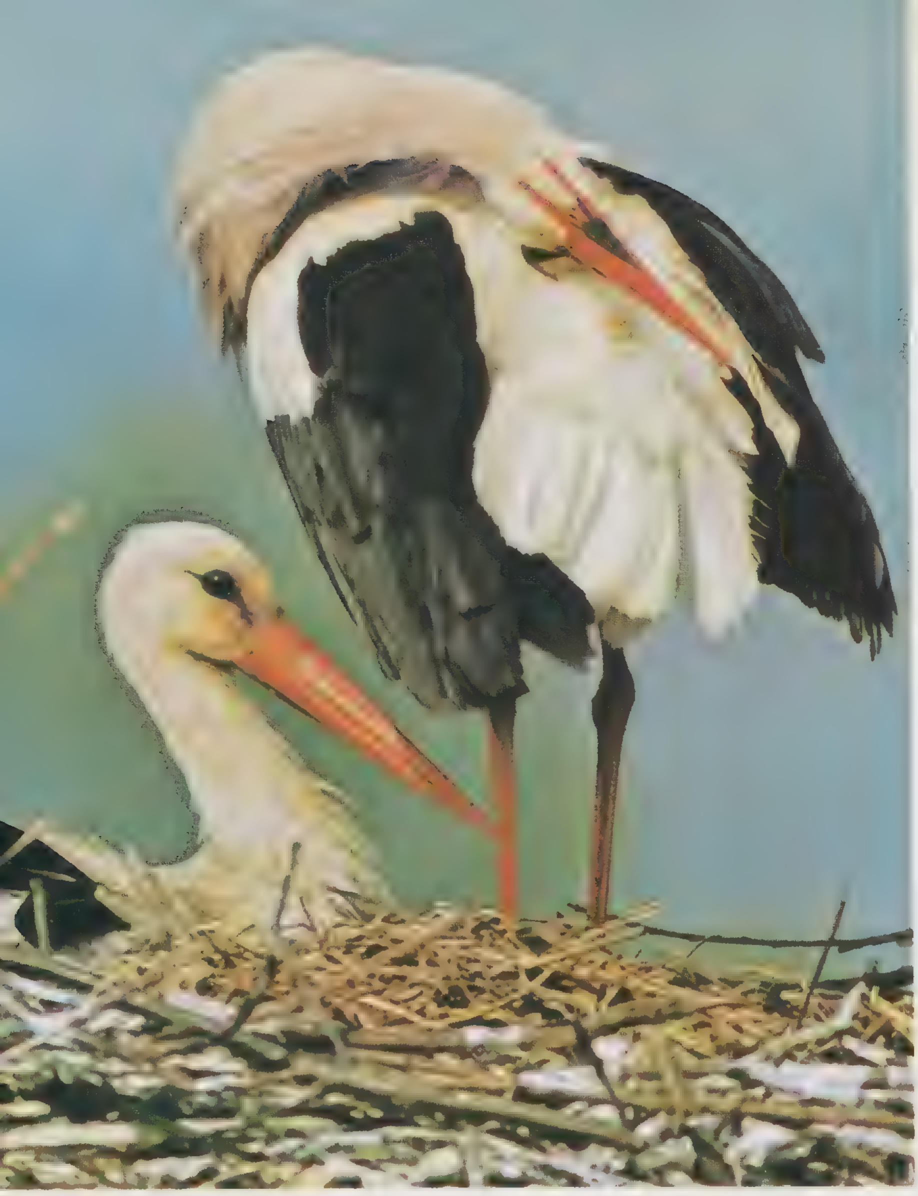
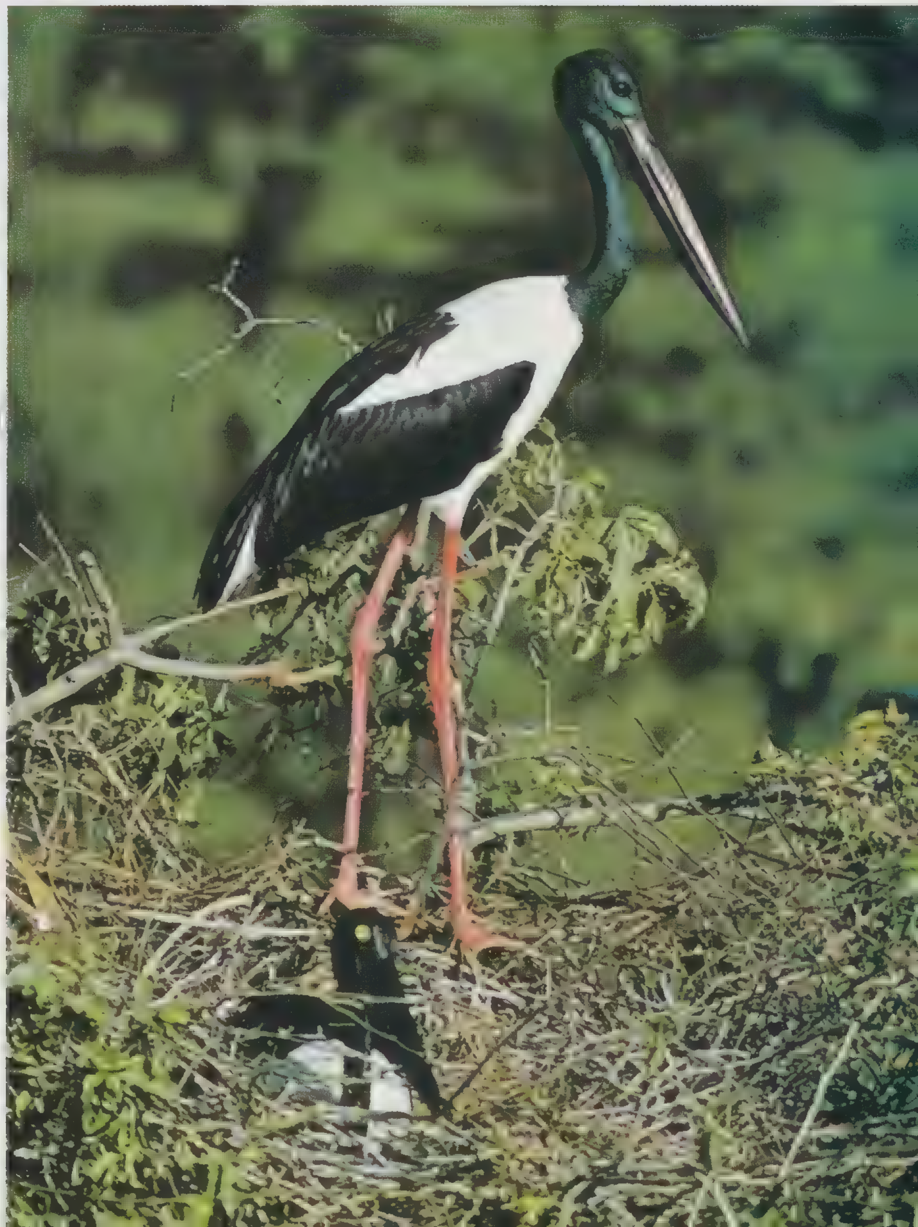


Plate VI.
White Stork, *Ciconia ciconia;* Milicz, Poland. Pair on nest: male sitting; female rubbing head on preen gland *(left)*.

Black-necked Stork, *Ephippiorhynchus* [=*Xenorhynchus*] *asiaticus;* Bharatpur, Rajasthan, India. Pair on nest: male, with dark eye, standing; female, with yellow eye, sitting *(right)*.



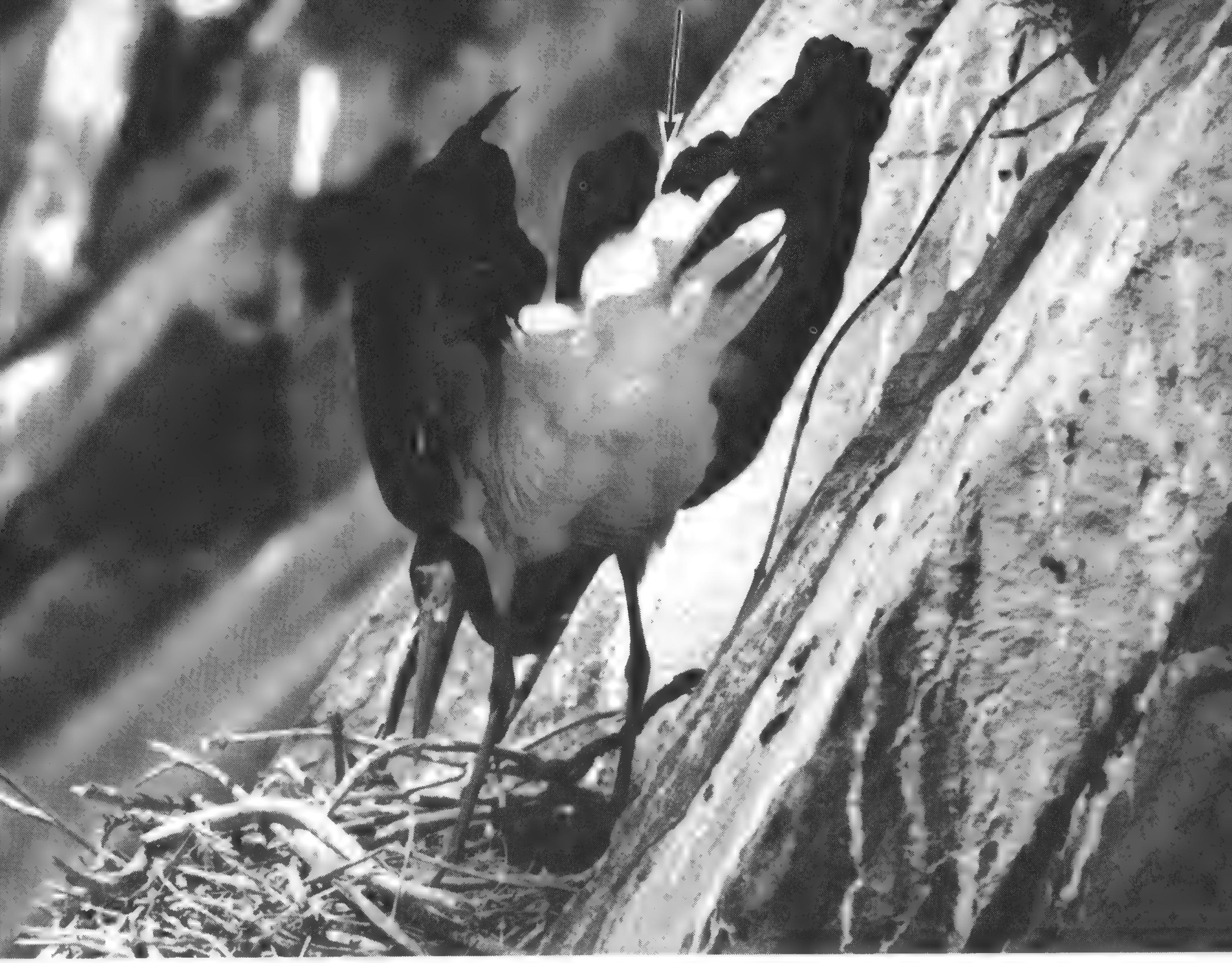


Figure 5. A male Abdim's Stork on his nest gives a Head-Shaking Crouch as a potential mate, out of sight on the left, approaches. Note the notched tail, marked by arrow (Lake Shala, Ethiopia, April 1967).

display appears to be most highly developed in the Abdim's Stork. In this species, the male bends forward with the tail high, the head low, and the body axis approximately 45 degrees below the horizontal (Figure 5). As the female draws near, the male bends his legs and crouches on the nest — as if sitting to incubate — and rapidly shakes his head from side to side in a "no" motion. The display usually ceases shortly after the female enters the nest.

The homologous display in the Woolly-necked Stork was observed only at Periyar Sanctuary, Kerala, India, at a nest where incubation was already in progress. The male crouched on the nest, with tail high, and shook his head as the female approached. The display appeared less striking than in Abdim's Stork but may have been given at low intensity, owing to lateness in the nesting season.

In the White Stork and the Black Stork, the Head-Shaking Crouch is even less ritualized. The male simply lies down in the nest — often with the luxuriant feathers of the lower foreneck erected — and shakes his head from side to side a number of times. I did not see the Head-Shaking Crouch in the Maguari Stork, perhaps because the nests that I had under close observation already contained young several weeks old. However, I predict that some observer will see the display during the courtship of this species.

As in other storks, the Up-Down is common after pair-formation. It is in this display that the "typical" storks show the greatest behavioral diversity.

The Up-Down is simplest in the Black Stork. Both members of a pair hold their heads forward, with their necks partially extended and bowed downward in the center (Plate IVa), and toss their bills slightly up and down while uttering a series of melodious bisyllabic whistles. At a nest in the Drakensberg area of Natal, South Africa, I once saw an adult Black Stork perform an Up-Down in which it threw the bill vertically upward and clattered a few times as it brought the bill down. Apparently, European Black Storks rarely clatter during the Up-Down (*cf.* Heinroth and Heinroth, 1924–1931; Siewert, 1932; Stoll, 1934); I witnessed no clattering at the Black Stork nests that I studied at Milicz, Poland, in 1969, even though I observed a number of Up-Downs. We need further observations to determine whether clattering during the Up-Down occurs more frequently in some populations of Black Storks — e.g., South African — than in others.

In the Abdim's Stork, the Up-Down is performed with the wings widely spread and held in that position (Plate IVb). The bird points its bill downward, utters a series of bisyllabic whistling notes, and then points the bill vertically upward and clatters rapidly.

The Woolly-necked Stork gives an Up-Down very similar in form and vocalizations to that of Abdim's Stork, except that the bill-clattering occurs with the bill held below the horizontal and the bird does not raise the bill to the vertical position.

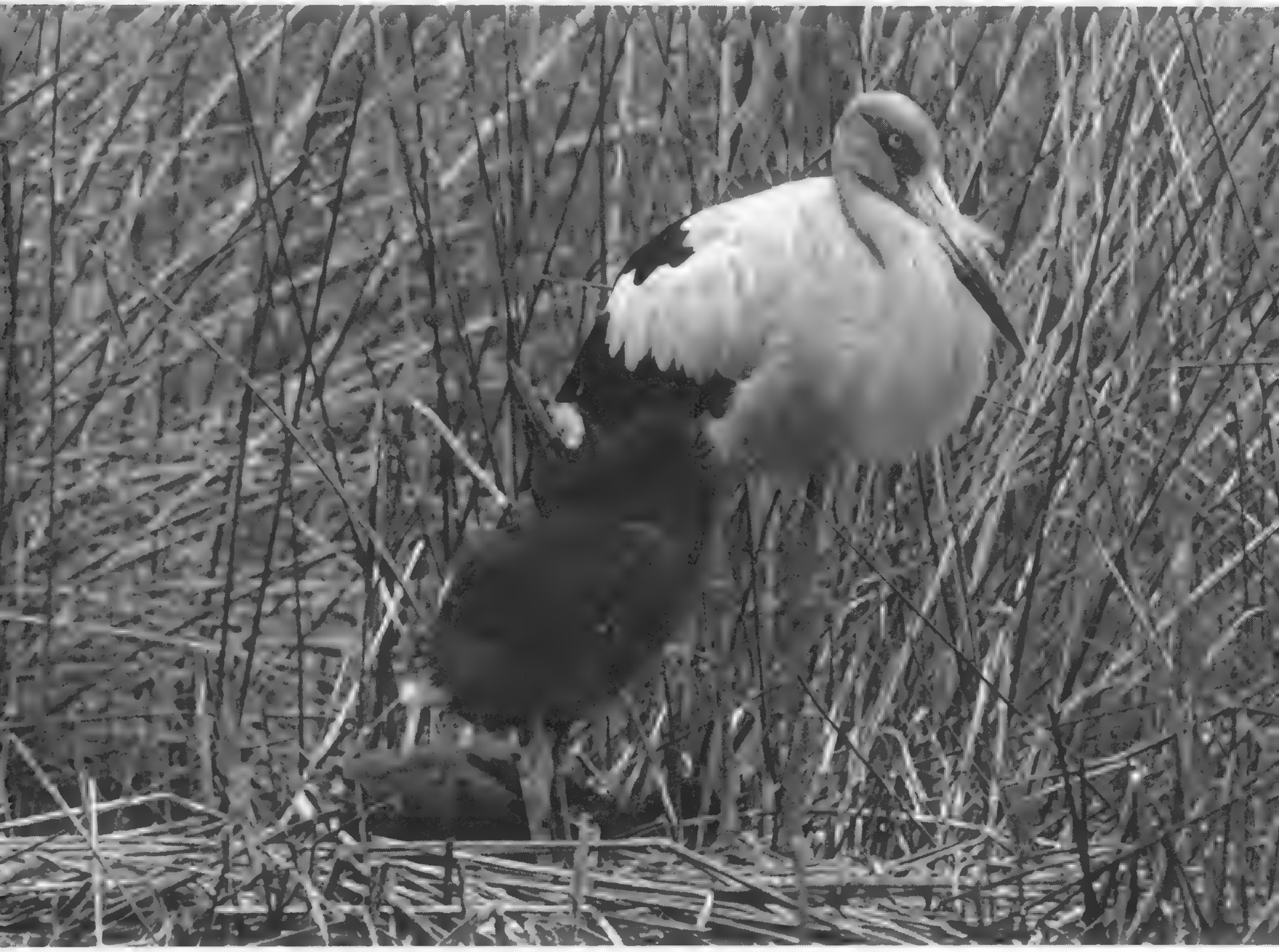


Figure 6. A nestling Maguari Stork gives an Up-Down, with head raised to behind the vertical, as adult stands nearby (Corrientes Province, Argentina, September 1969).

Up-Down displays of the Maguari Stork were difficult to observe at the nests I studied in Argentina because the nests were built on the ground in extensive marshes and were surrounded by high reeds and other vegetation. The few Up-Downs that I saw consisted of the bird throwing its head upward, so that the bill was approximately vertical, and rapidly clattering the mandibles six to ten times. Immediately before or after clattering, the bird uttered several wheezy, bisyllabic whistles, similar to those given by the Black, Abdim's, and Woolly-necked Storks, but deeper in pitch and slower in tempo. I observed many Up-Downs at close range in nestlings of the Maguari Stork between two and five weeks old. The young usually displayed when a parent landed at the nest, and also when I approached close to their nests. The nestlings threw their heads upward, until their bills were vertical or behind vertical, and "clattered" their bills rapidly several times (Figure 6). Owing to the softness of the mandibles of the nestlings, very little clattering sound was produced. These Up-Downs in the Maguari Stork nestlings looked remarkably like those described and illustrated in the White Stork nestlings by Schüz (1942:10–11).

The Up-Down of the White Stork is one of the most highly developed — as well as the best known — of any stork. The bird clatters its bill rapidly and loudly and throws its head vertically upward, then all the way back until the crown is resting on the back and the bill is pointed down the back toward the tail (Figure 7), then forward again to the normal position. Clattering continues throughout the entire display.

I observed Copulation-Clattering only in the Black, Abdim's, and White Storks. It was similar in these three species. The male clatters his bill rapidly and rather softly in the long throat feathers of the female, and the female opens her wings only to the "wrist" during the copulation (Figure 8). Thus, Copulation-Clattering, in the "typical" storks that I observed, differed from homologous behavior in the wood storks and openbills in that the male did not beat his bill forcefully back and forth against the bill of the female. The female did not hold her wings widely spread as do the females of the genera *Mycteria, Ibis, Xenorhynchus,* and *Leptoptilos.*

Other Characteristics. — The "typical" storks are distinguished from all other storks by the following morphological features: (1) bill rather thin and essentially straight; (2) luxuriant ruff of feathers on lower foreneck; (3) feathered head and neck, with bare skin on lores and around eyes; (4) plumage pattern in various combinations of white and iridescent black.

The Black Stork is predominantly iridescent black with white sides and abdomen; its tail is composed of 12 black rectrices of approximately equal length. Abdim's Stork, patterned much like the Black Stork but smaller in body size, has the central pair of rectrices about 20 millimeters shorter than the other rectrices, giving the margin of the black tail a notched appearance when spread (Figure 5). The Woolly-necked Stork has iridescent black body plumage with a white abdomen, nape, and neck; it has a deeply forked black tail, in which the rectrices diminish in length from the outermost inward, and elongated, stiffened, white undertail coverts that protrude beyond the true rectrices. The Maguari Stork is predominantly white with black flight feathers in the wings and a deeply forked black tail similar to the Woolly-necked. The White Stork has a plumage pattern similar to the Maguari; however, it is unique among storks, except for the all-white Jabiru Stork (see below), in having a white tail with 12 rectrices of approximately equal length.

The Saddlebill and Black-necked Storks
(Plates VIb and VIIa)

The Saddlebill Stork (*Ephippiorhynchus senegalensis*) of tropical Africa and the Black-necked Stork (*Xenorhynchus asiaticus*) of tropical Asia and Australia are rather uncommon birds throughout most of their ranges. Both are solitary breeders and probably remain mated with the same partner during successive seasons, for pairs are frequently seen together even outside the breeding season.

Social Displays.—As is the case in other storks that apparently retain the same mate for successive seasons, the Saddlebill and Black-necked Storks are relatively undemonstrative at the nest. Some pairs gave few or no displays to each other during my long periods of observation.

Before breeding began, members of a pair often foraged together along the borders of lakes or in shallow-water marshes. In these situations, the male — and occasionally the female as well — performed an action which I believe to be a social display and which I have termed the Flap-Dash. When

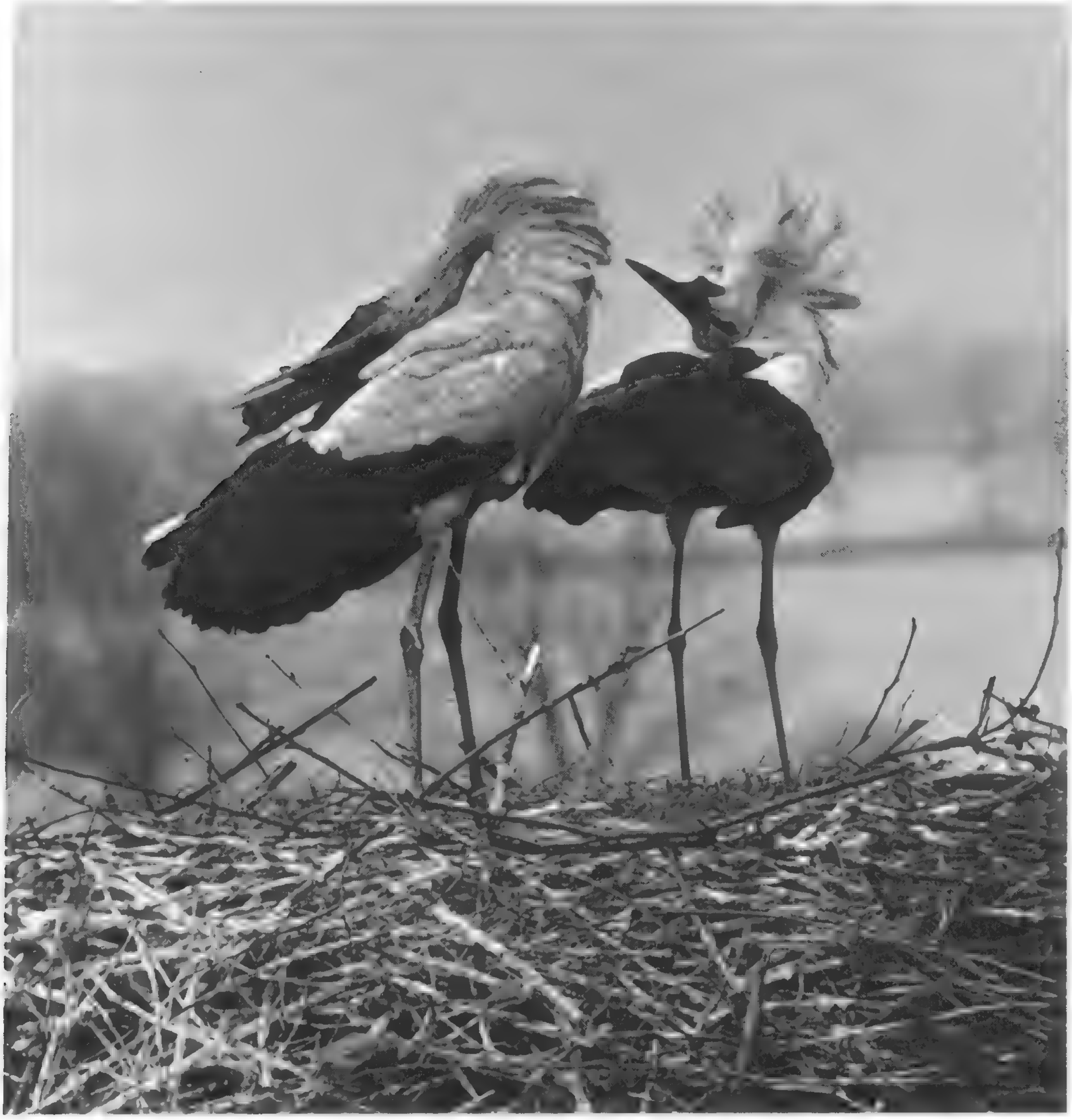


Figure 7. A pair of White Storks in the "full-back" position during Up-Down on the nest; the male is on the left (Milicz, Poland, April 1969).

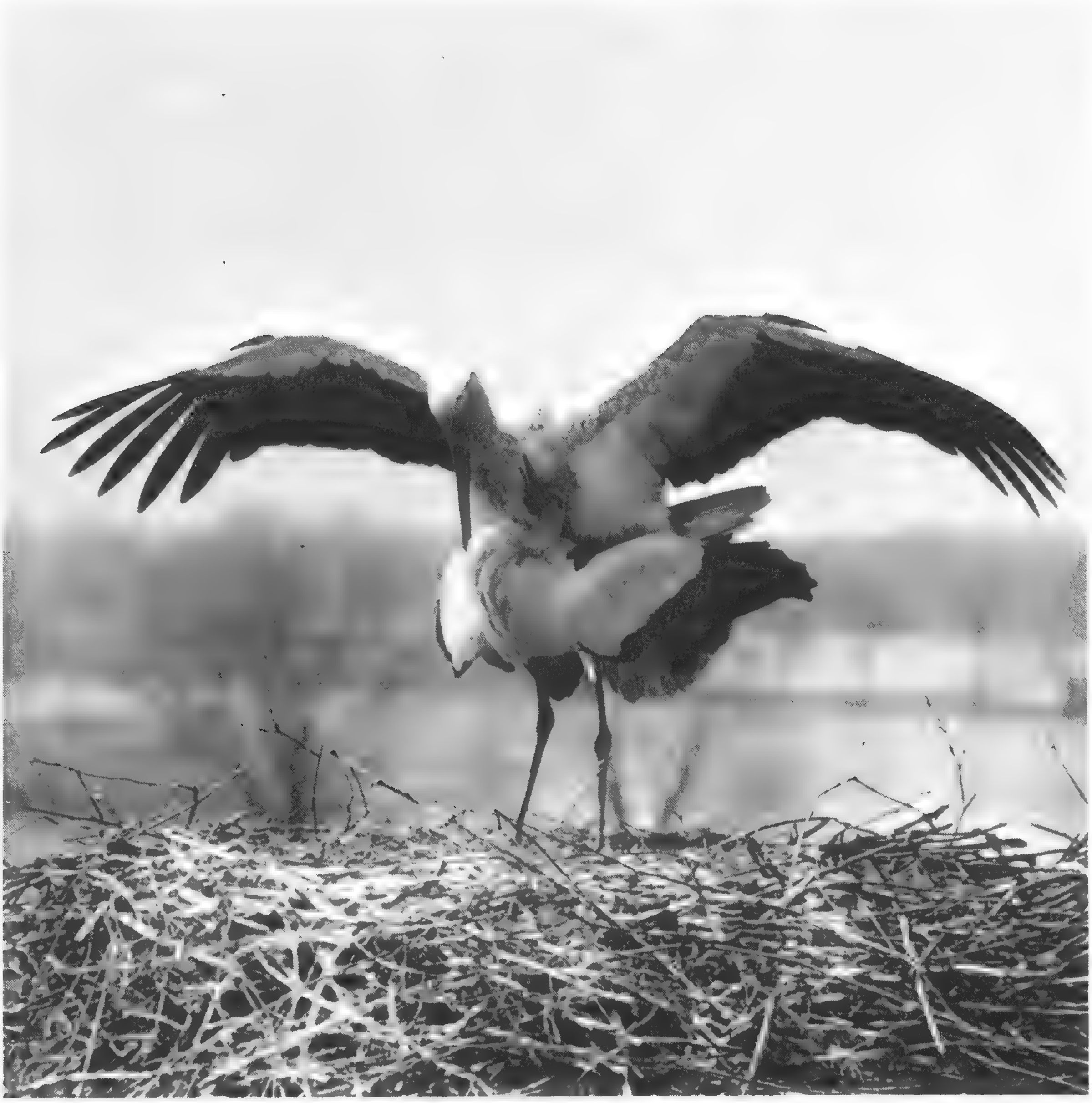


Figure 8. Copulation Clattering in White Storks. Note that the female keeps her wings nearly closed during the copulation (Milicz, Poland, April 1969).

the pair foraged together, one suddenly stood erect and dashed wildly through the water, flapping its wings vigorously. It dashed away from its mate, then turned and dashed back, often running up to within one to two meters of the other bird and standing there erect for several seconds with wings widely extended, before closing the wings and continuing to forage.

When I first observed this action in the Saddlebill, I thought that the performing bird was chasing active prey about in the shallow water. However, I have since seen the Flap-Dash several times in the Saddlebill, Black-necked, and Jabiru Storks (*Jabiru mycteria*) — see below — and I am now convinced that it is a social display rather than merely a foraging maneuver, although it may be derived from the latter. For one thing, the "chase" rarely resulted in prey being captured. Although the bird did sometimes make a grab into the water, it usually came up with only a piece of aquatic vegetation. Secondly, the bird performing the Flap-Dash seemed to pay more attention to its mate than to anything in the water and often ended the display by running up to its partner.

The Up-Down in the Saddlebill has apparently never been described. Although I watched an active nest near Kisumu, Kenya, for nearly three months during two breeding seasons, I never saw an Up-Down given. This may have been due to the fact that in both years I was not present to witness the first two weeks of the breeding season — i.e., the occupation of the nest, nest-repair, copulation, and egg-laying — which, in other storks, is the period of most intense social display.

I saw the Black-necked Stork in India perform Up-Downs a number of times on a nest or potential nest site. Hume and Oates (1890:266) saw Up-Downs given by a pair of birds on the ground. In this spectacular display, both birds stand erect, facing each other, and spread their wings widely to the sides, so that their wing-tips are almost touching. They then clatter their bills rapidly and loudly, while holding them in approximately the normal position, and flutter their wings rapidly, so that the tips move through an arc of about 20 centimeters. Each time I saw the Up-Down given by the Black-necked Stork, both members of the pair took part; on one occasion, I saw it given by a pair on a nest site when a third individual of undetermined sex flew overhead.

Other Characteristics. — In general morphology, the Saddlebill and Black-necked Storks (Plates VIb and VIIa) are characterized by slender bodies, long and slightly recurved bills, and white flight feathers in the wing. They differ from each other mainly in the coloration of the bill and fleshy parts. They are the only two species of storks with conspicuous sexual dimorphism: males have dark brown irises, females lemon-yellow ones.

The Jabiru Stork
(Plate VIIb)

The Jabiru Stork (*Jabiru mycteria*) breeds from British Honduras southward throughout much of South America, east of the Andes, to northern Argentina. It is the largest stork in the New World, and the only member of the family that has an all-white plumage.

Social Displays. — Like the Saddlebill and Black-necked Storks, the Jabiru nests solitarily and may remain with the same mate for successive seasons, although firm evidence to support this hypothesis is lacking. Also, like the Saddlebill and Black-necked Storks, the Jabirus that I observed in Argentina were, for the most part, rather undemonstrative at the nest.

In one foraging pair of Jabirus — observed near Mburucuyá, Corrientes Province, Argentina, in August 1969 — I witnessed a Flap-Dash that was strikingly similar to those seen in Saddlebill and Black-necked Storks of the Old World. The displaying male dashed through the shallow water of the feeding area with flapping wings and during the display he ran up to within two meters of the female.

At the six active Jabiru nests that I watched (Kahl, 1971a), I observed the Up-Down on only two occasions at one nest. In the Up-Down, the birds stand in the nest facing each other and clatter their bills rapidly and loudly. During clattering they raise their bills periodically to about the horizontal and then lower them again to the normal position; their heads and necks sway slowly from side to side. As the heads and necks of both birds sway, their bills pass over and under each other. The Up-Down of the Jabiru shows definite affinities with the similar display in the Black-necked Stork, but in the Jabiru the wings are not spread and fluttered.

Other Characteristics. — The Jabiru shares a number of morphological and behavioral traits with the Saddlebill and Black-necked Storks and also

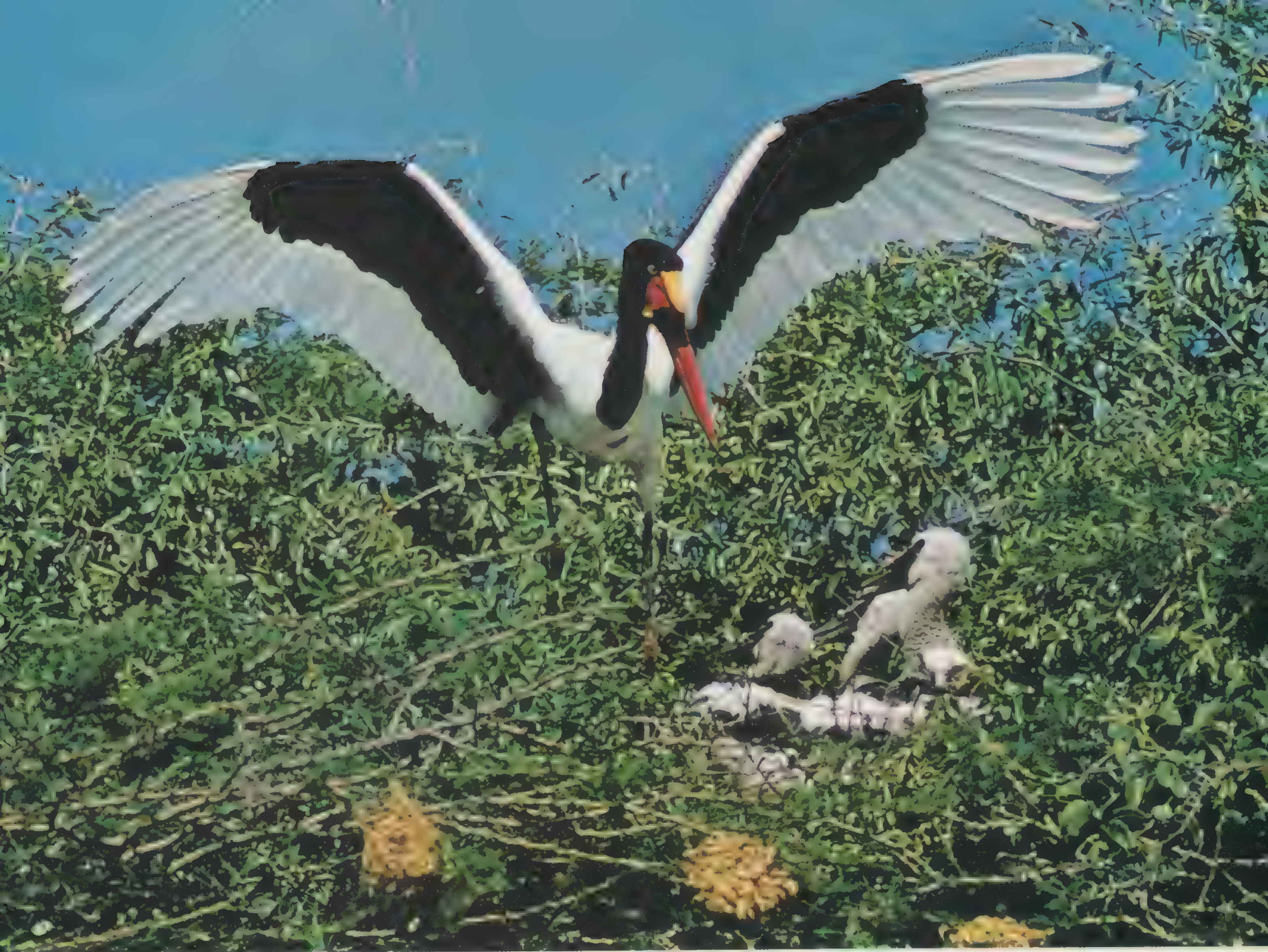
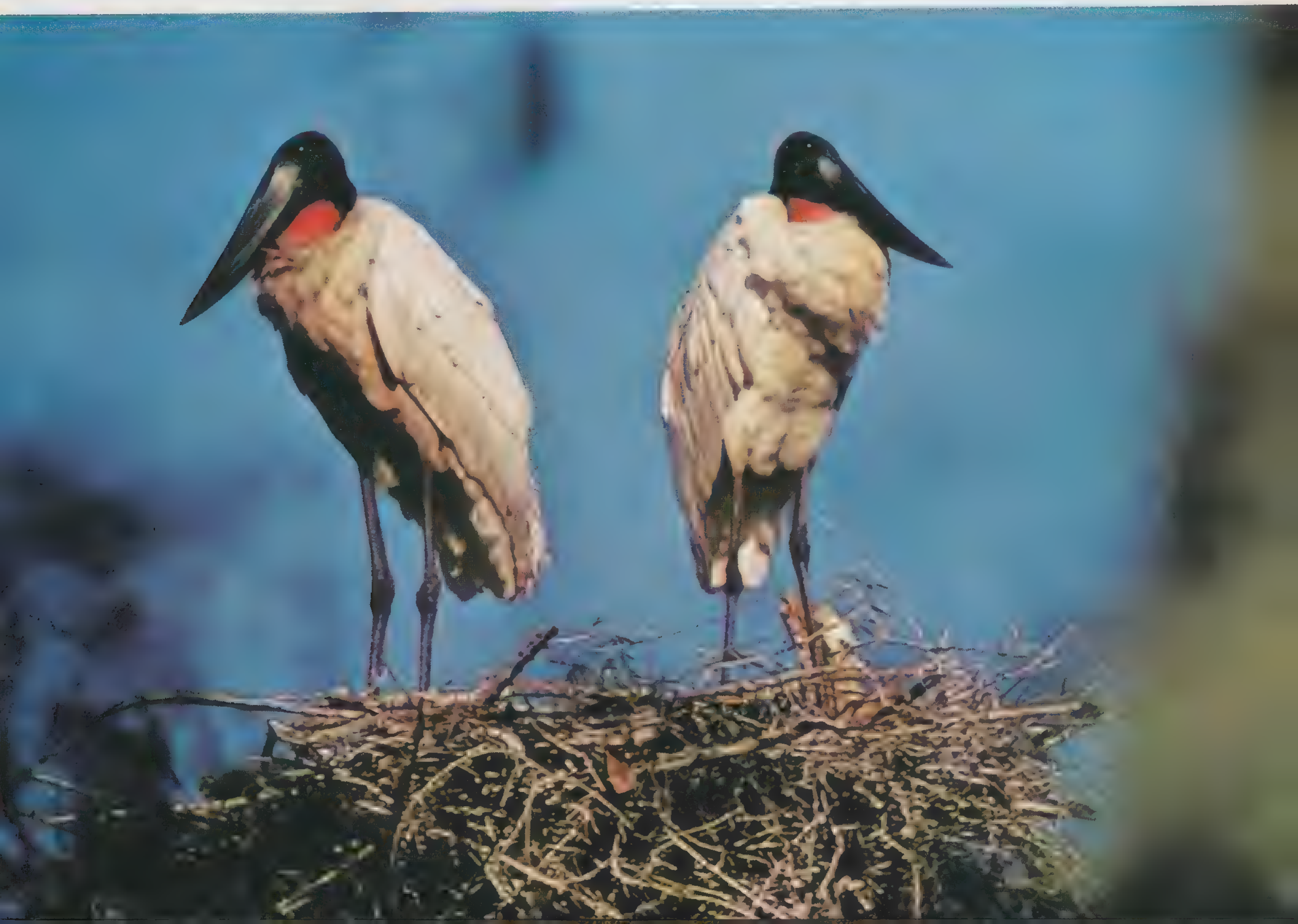


Plate VII. Saddlebill Stork, *Ephippiorhynchus senegalensis;* Kisumu, Kenya.
Adult female landing on nest containing three nestlings about 45 to 50 days old *(above).*

Jabiru Stork, *Jabiru mycteria;* Santa Teresa, Corrientes, Argentina.
Pair standing on nest; male on left *(below).*



with the Marabou Stork and adjutant storks, (described below). Since I have treated these traits in another paper (Kahl, 1971a), I will not discuss them fully here. A summation of the available evidence suggests that although the genus *Jabiru* appears to be most closely related to *Ephippiorhynchus* and *Xenorhynchus,* it occupies a taxonomic position intermediate between those genera and the genus *Leptoptilos.*

The Marabou and Adjutant Storks
(Plates VIII and IXa)

The Marabou Stork (*Leptoptilos crumeniferus*) occurs throughout tropical Africa; the Greater Adjutant (*L. dubius*) ranges from India to Indochina, breeding mainly in southern Burma; and the Lesser Adjutant (*L. javanicus*) inhabits Ceylon, southern and northeastern India to Indochina, Borneo, and Indonesia.

Social Displays. — A full account of the behavior of these three species has been presented elsewhere (Kahl, 1966; in press, a). In most aspects of display and other behavior, the species of *Leptoptilos* are rather similar. However, they differ significantly from each other in two important social displays.

During courtship, and occasionally later, females typically land near lone males on nest sites and approach them in the Balancing Posture. In this display, a female Marabou stands with body nearly horizontal, bill pointed downward, and wings held widely spread. The Balancing Posture in the Greater Adjutant appeared similar (Plate VIIIb). In the Lesser Adjutant, the homologous display begins in the same way; then the female bends her legs, lowers her head and neck, and clatters the mandibles loudly five to six times while lifting the bill forward and upward with a slight "scooping" motion. This pronounced difference in the Balancing Postures of the Greater and Lesser Adjutants may provide the isolating mechanism that prevents hybridization in areas where both species nest together in large mixed colonies — for example, in Burma (see Smythies, 1953).

After pair-formation, all three species of *Leptoptilos* give frequent Up-Downs whenever one member of the pair returns to the nest after an absence. In the Marabou, the bird first throws its head upward with the bill nearly vertical (Plate IXa) and utters a series of loud, high-pitched squeals and deep-throated "moo's." Then it lowers its head, points the bill vertically downward, and clatters loudly. The two adjutant storks initiate the Up-Down in the same way, but they keep their bills in the upward position while clattering.

Other Characteristics. — Of the three species in the genus, the Lesser Adjutant is the least specialized in its morphology and behavior, and it apparently scavenges less frequently than either the Greater Adjutant or the Marabou (Ali and Ripley, 1968:108; Kahl, 1970). And the large, pendant, inflatable throat sac of the other two species is not well developed in the Lesser Adjutant. In some morphological characters — such as bill shape, coloration and external structure of the throat-sac — the Lesser Adjutant shows more affinities with the Jabiru than do the other two species of *Leptoptilos.*

Discussion

Since the classification of Peters (1931), few attempts have been made to clarify the systematics of the Ciconiidae. Verheyen (1959) revised the group largely on the basis of comparative osteology.

TABLE 2

Proposed Changes in Stork Nomenclature and Sequence

Peters' classification (1931)	*Proposed classification*
Family Ciconiidae	Family Ciconiidae
Subfamily Mycteriinae	Tribe Mycteriini
Mycteria americana	*Mycteria americana*
Ibis ibis	*Mycteria cinerea*
Ibis leucocephalus	*Mycteria ibis*
Ibis cinereus	*Mycteria leucocephala*
Subfamily Ciconiinae	*Anastomus oscitans*
Anastomus oscitans	*Anastomus lamelligerus*
Anastomus lamelligerus	Tribe Ciconiini
Sphenorhynchus abdimii	*Ciconia nigra*
Dissoura episcopus	*Ciconia abdimii*
Ciconia ciconia	*Ciconia episcopus*
Ciconia nigra	*Ciconia maguari*
Euxenura galeata	*Ciconia ciconia*
Xenorhynchus asiaticus	Tribe Leptoptilini
Ephippiorhynchus senegalensis	*Ephippiorhynchus asiaticus*
Jabiru mycteria	*Ephippiorhynchus senegalensis*
Leptoptilos dubius	*Jabiru mycteria*
Leptoptilos crumeniferus	*Leptoptilos javanicus*
Leptoptilos javanicus	*Leptoptilos dubius*
	Leptoptilos crumeniferus

Until the present study, the literature contained little information on the ethology or ecology of most storks under natural conditions, the major exception being the work on the White Stork (*C. ciconia*). In this paper I attempt to arrange the storks in a natural classification (Table 2), based on studies of the living birds in nature, as well as on morphological data.

Peters (1931) divided the Ciconiidae into two subfamilies — Mycteriinae and Ciconiinae. I agree with Verheyen (1959:29) that the differences between the groups are too small to justify the separation into subfamilies. Perhaps it is wise to leave the category of subfamily open until further information becomes available on the taxonomic position of the Shoebill, *Balaeniceps rex* (cf. Mayr and Amadon, 1951:6); see Plate IXb. Furthermore, I agree with Verheyen that the storks should be divided into tribes; but I would place them in three, rather than four, tribes: Mycteriini, Ciconiini, and Leptoptilini. My arrangement of species and genera within the tribes also differs markedly from that proposed by Verheyen.

At the generic level, I suggest several changes from the classification of Peters (1931). In modern taxonomic thinking, the genus reflects close relationships between species, whereas the species reflects biologically significant differences—*i.e.*, reproductive isolation—between populations. The extensive use of monotypic genera in groups containing closely related species defeats the first of these objectives.

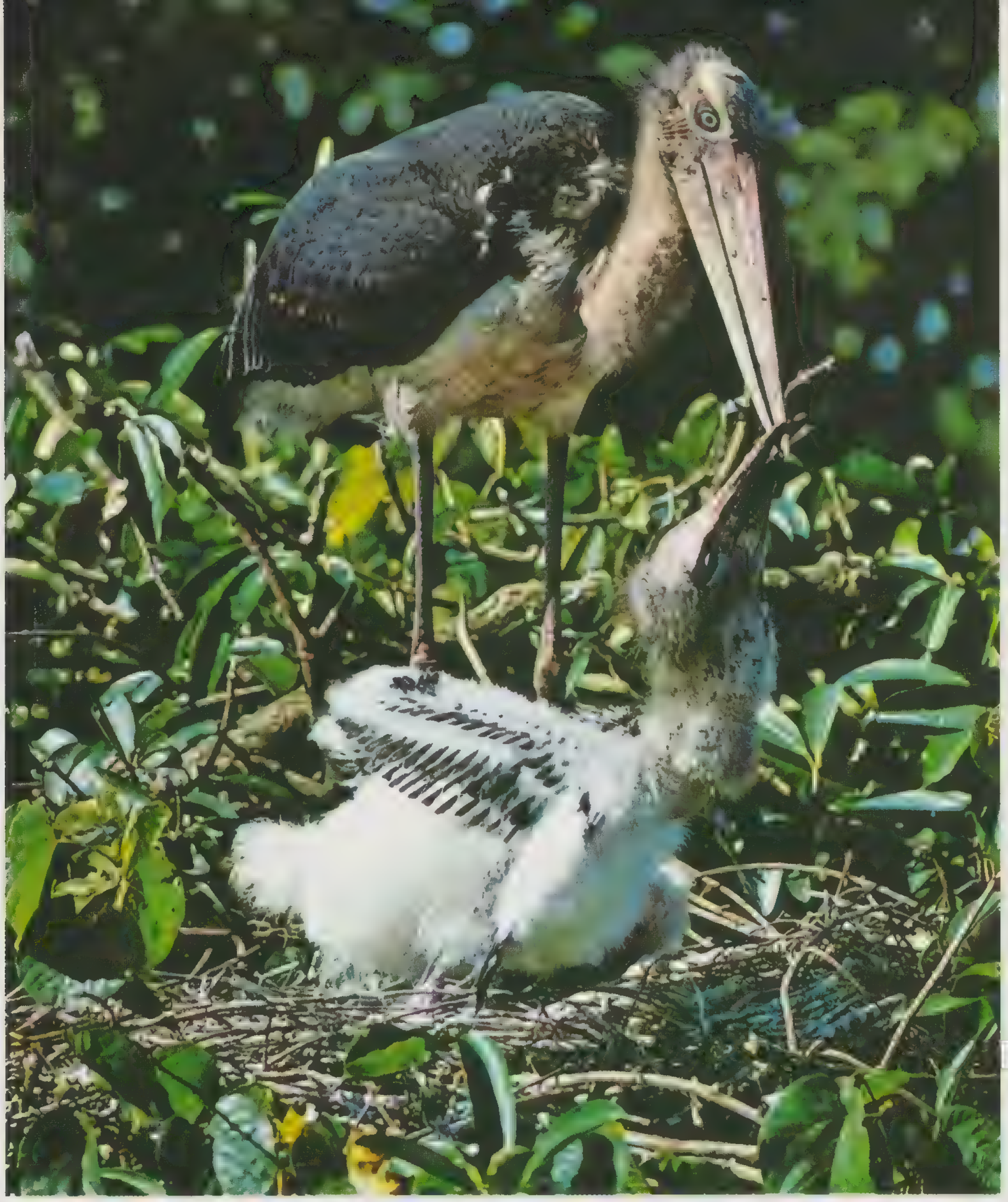
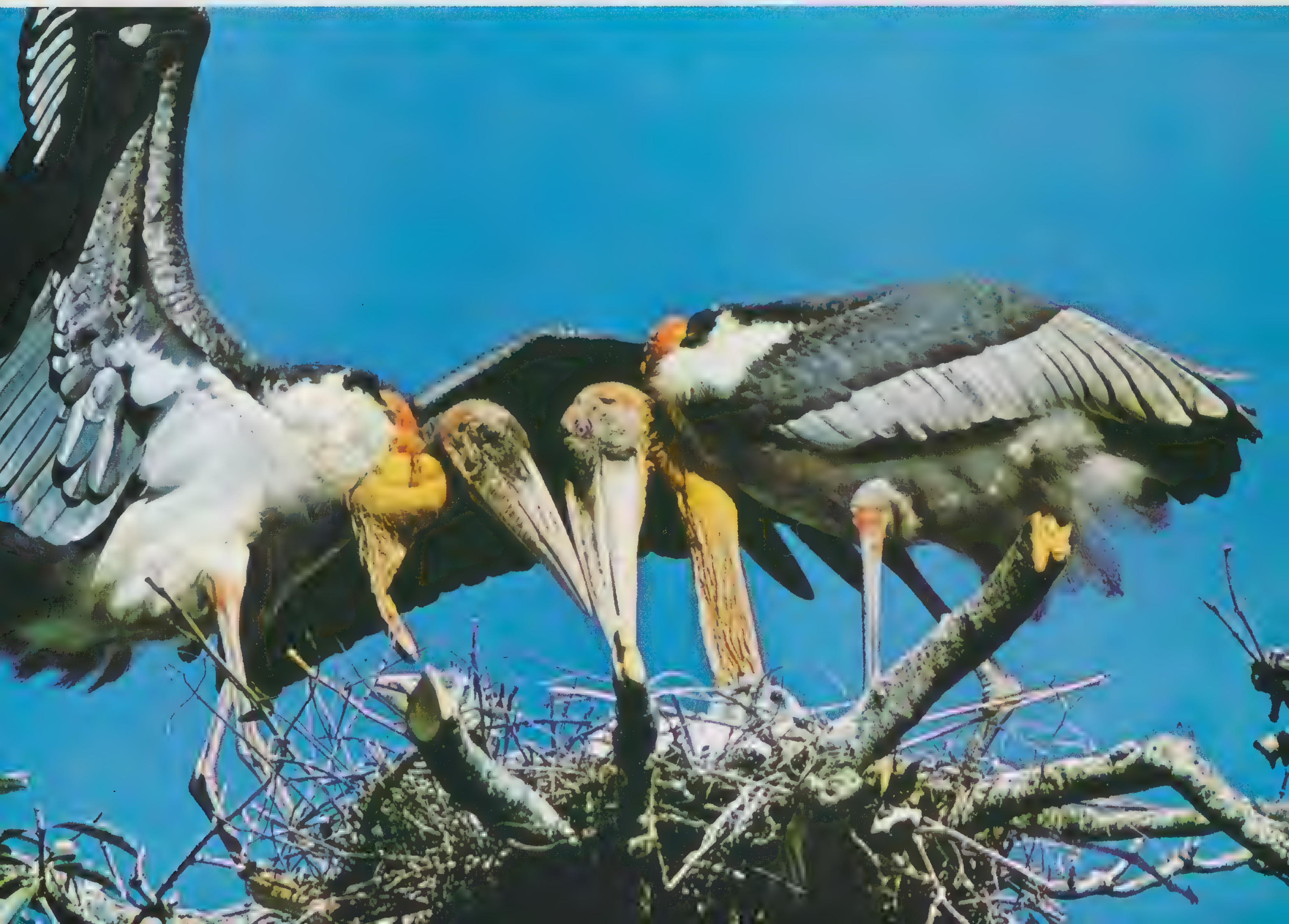


Plate VIII.
Lesser Adjutant Stork,
Leptoptilos javanicus;
Nowgong, Assam, India.
Adult preparing to feed
begging nestling, about
40 days old *(left).*

Greater Adjutant Stork,
Leptoptilos dubius;
Kaziranga, Assam, India.
Pair on nest; female on
left in Balancing Posture;
two nestlings about 35
to 40 days old *(below).*



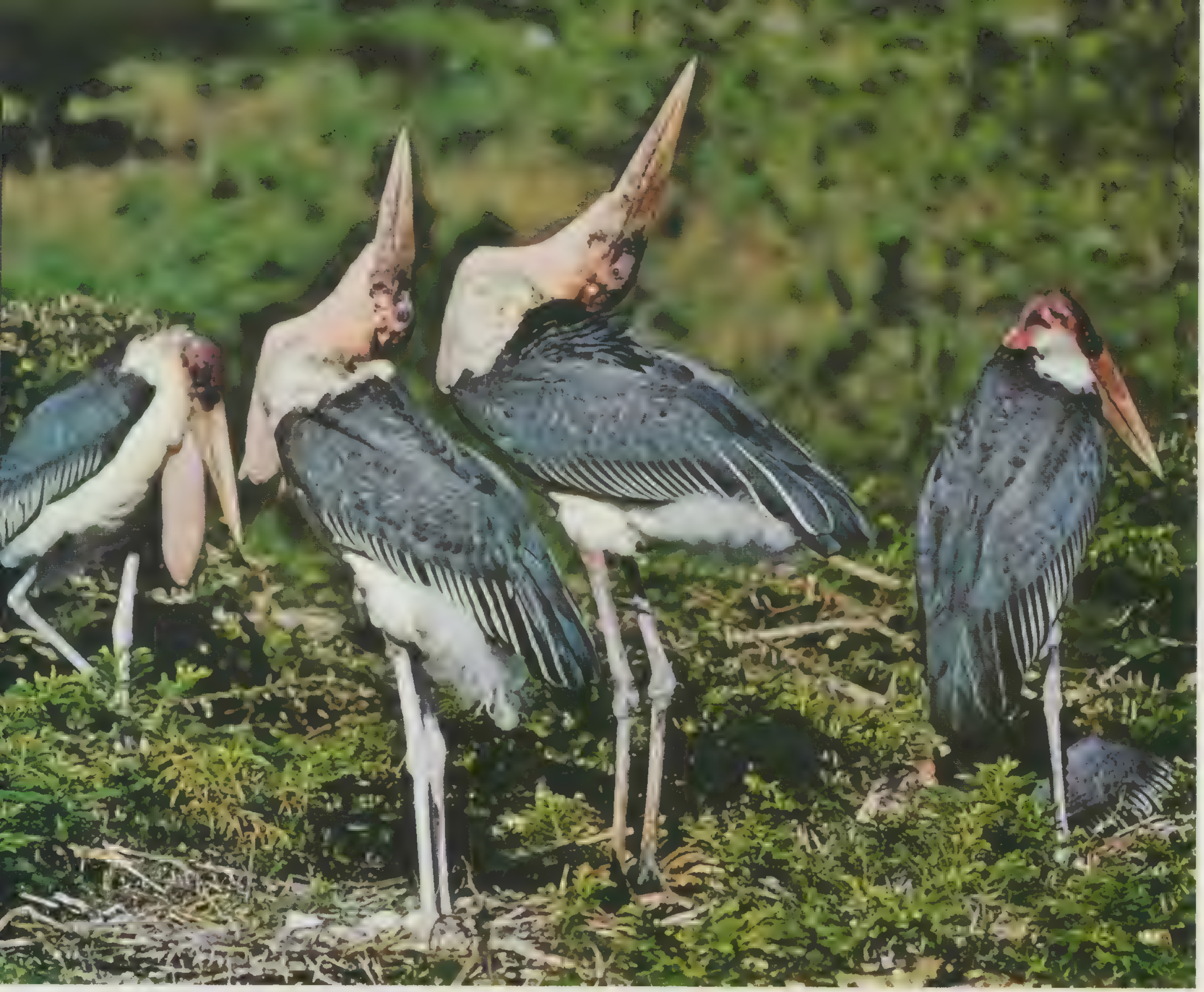


Plate IX. Marabou Stork, *Leptoptilos crumeniferus;* Kitale, Kenya.
Pair performing mutual Up-Down display; male on right *(above).*

Shoebill, *Balaeniceps rex;* Lira, Uganda.
A possible relative of the storks. Little is known of its behavior *(below).*

The wood storks are a relatively uniform group, both behaviorally and morphologically. *Mycteria americana,* the American Wood Stork, differs from the three species of *Ibis* (Plates I and II) mainly in the lack of feathering on the hind head and neck of the adult — immature *M. americana* have feathered heads and necks, similar to *Ibis* — and in quantitative aspects of some displays. Thus, I see no justification for maintaining *Mycteria* as a monotypic genus and feel that it should be considered synonymous with *Ibis.* The name *Mycteria* (1758) has priority and, thus, the three species of *Ibis* (1799) become *M. ibis* (Yellow-billed Stork), *M. leucocephala* (Painted Stork), and *M. cinerea* (Milky Stork), respectively. Since I can see no objective basis for deciding which of the wood storks is "most primitive," I suggest arranging the species within the genus *Mycteria* in alphabetical order (Moreau, 1961).

The openbill storks (*Anastomus*) show closer behavioral ties with the wood storks (*Mycteria*) than with any other group. Both genera show an Up-Down display with extended necks, gaping bills, and lack of true bill-clattering. Furthermore, during the Copulation Clattering of both *Anastomus* and *Mycteria,* the male beats his bill roughly back and forth against the bill of the female. The openbills were placed in a separate tribe by Verheyen (1959) (who also commented on their affinities with *Mycteria* and *Ibis*) mainly on the basis of cranial osteology. I consider skull structure in the openbills to be of dubious taxonomic value, owing to the likelihood that it is adaptively related to their specialized feeding techniques (Kahl, 1971b). For these reasons, I favor placing *Anastomus* in the tribe Mycteriini. The two openbills differ from each other mainly in plumage pattern. Since the plumage of *A. oscitans* (the Asian Openbill) appears most similar to the other storks, I consider it the most primitive of the two species.

When examined from the standpoint of both behavior and morphology, *C. ciconia* (White Stork) and *C. nigra* (Black Stork) differ from each other in a number of ways. Now that more data are available on the behavior of *Sphenorhynchus abdimii* (Abdim's Stork), *Dissoura episcopus* (Woolly-necked Stork), and *Euxenura galeata* (Maguari Stork), it is apparent that *S. abdimii* shows closer affinities with *C. nigra,* and that *E. galeata* shows closer affinities with *C. ciconia.* Moreover, *D. episcopus* shows a relationship to both *S. abdimii* and *E. galeata.* Thus, it seems that *Sphenorhynchus, Dissoura,* and *Euxenura* are probably more closely related to *C. nigra* and *C. ciconia,* respectively, than *C. nigra* and *C. ciconia* are to each other.

For example, four of the five species — all except *C. ciconia* — utter a similar whistling vocalization during the Up-Down. At least four of the five species show a similar Head-Shaking Crouch (not observed in *E. galeata,* probably owing to lateness in the season); and in the same four species, the female opens her wings only to the wrist during copulation. The structure of the tail also gives a clue to relationships within the group of "typical" storks: *C. nigra* with black rectrices of approximately equal length; *S. abdimii* with a slightly notched black tail; *D. episcopus* and *E. galeata* with deeply forked black tails and elongated white undertail coverts; and *C. ciconia* with white rectrices of approximately equal length.

I suggest combining these five species in the genus *Ciconia,* eliminating the genera *Sphenorhynchus, Dissoura,* and *Euxenura;* a similar proposal was made by Delacour and Mayr (1945:105). The five species of the genus *Ciconia* compose the tribe Ciconiini. I concur with Hellmayr and Conover (1948:245) that the specific name of the Maguari Stork should be *maguari* rather than *galeata.* The original description for *galeata* was confusing — referring to both the stork and an egret — and, thus, should be discarded from the nomenclature.

Ephippiorhynchus senegalensis (Saddlebill Stork) and *Xenorhynchus asiaticus* (Black-necked Stork) are strikingly similar in behavior and in morphology, with the principal exception of soft-part coloration. They share the sexual dimorphism in iris color, which is shown by no other species of stork. Both show the Flap-Dash display, and their other patterns of general behavior are closely similar. Unfortunately, the Up-Down display in *E. senegalensis* has not been described; I predict that it will be found to correspond closely to that of *X. asiaticus.* I see little justification for retaining both species in monotypic genera and propose that they be combined under *Ephippiorhynchus,* which has "line-priority" in Bonaparte (1857:106). I have placed *E. asiaticus* first in the linear sequence because of its less elaborate pattern of soft-part coloration.

As mentioned earlier in this paper and in Kahl (1971a), *Jabiru mycteria* (Jabiru Stork) — while most closely related to *Ephippiorhynchus* — also shows characters that suggest an affinity with the genus *Leptoptilos.* Because of its intermediate position and rather clear cut differences from both *Ephippiorhynchus* and *Leptoptilos,* I recommend that *Jabiru* be retained as a monotypic genus.

Few people familiar with the birds will deny that the genus *Leptoptilos* is a distinct group. *L. javanicus* (Lesser Adjutant Stork) appears to be the least specialized of the three species. *L. dubius* (Greater Adjutant Stork) shows some behavioral similarities to *L. javanicus* — for example, in the Up-Down display — but, overall, it appears more closely related to *L. crumeniferus* (Marabou Stork). However, owing to the pronounced differences in the Up-Down between *L. dubius* and *L. crumeniferus,* I reject the suggestion of some authors (e.g., Meinertzhagen, 1951:448) that they be considered races of one species. The Up-Down appears to be of importance in maintaining the pair-bond throughout the breeding season, and I feel that major differences in the display would function as isolating mechanisms in the event that *L. dubius* and *L. crumeniferus* ever became sympatric.

Owing largely to the link provided by *Jabiru,* the genera *Ephippiorhynchus* (includes *Xenorhynchus*), *Jabiru,* and *Leptoptilos* are combined in the tribe Leptoptilini.

Summary

This paper is a synopsis of an 11-year investigation of the comparative behavior of the storks and presents data gathered at active nests of all 17 living species.

Based on behavioral data — particularly ritualized social displays — in addition to morphological characters, I propose several changes of nomenclature and sequence in the classification of the Ciconiidae (see Table 2). I suggest the elimination of subfamilies and the erection of three tribes: Mycteriini, Ciconiini, and Leptoptilini. The following genera are based on insufficient differences and should be synonymized as follows: *Ibis* (synonymized with *Mycteria*); *Sphenorhynchus, Dissoura,* and *Euxenura* (synonymized with *Ciconia*); and *Xenorhynchus* (synonymized with *Ephippiorhynchus*).

According to my analysis, the family Ciconiidae includes three tribes, six genera, and 17 species, as opposed to the two subfamilies, 11 genera, and 17 species of Peters (1931).

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VOCALIZATIONS OF THE CHUCK-WILL'S-WIDOW AND SOME RELATED BEHAVIOR

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Photographs by the authors

No group of birds has been more shrouded in secrecy and legend than the marvellously camouflaged, day-sleeping, forest floor-inhabiting goatsuckers of the family Caprimulgidae. For many years after the arrival of English-speaking colonists in the New World there was persistent confusion concerning the sources of the varied vocalizations of these birds, and even about their identities (McAtee, 1948). Long after the number of species and their morphological characteristics were established, confusion endured concerning the number, nature, and function of the sounds produced by each (e.g., Sprunt, 1940; Tyler, 1940). This is only natural: not many students of goatsuckers have remained long in the moonlit forests and clearings at night, and the few who have often found the sounds they heard difficult to attribute to a particular species and all but impossible to associate with behavioral patterns. Of the few preliminary efforts to list the sounds of any of these species, by far the best is Harper's (1938) brief, widely overlooked account of the Chuck-will's-widow (*Caprimulgus carolinensis*).

Because of the many gaps in our knowledge of these birds, we tried to make the most of our opportunities to study two species of goatsuckers. Near our home in Douglas County, northeastern Kansas, the Whip-poor-will (*Caprimulgus vociferus*) and the Chuck-will's-widow are locally common and occur more or less side by side in the same forests and adjacent clearings. From 1963 through 1968, as opportunity permitted, we studied these birds from their arrival in spring until the cessation of song in late summer. We made intensive observations almost nightly, weather permitting, in 1963, 1964, and 1965.

Our data for the Chuck-will's-widow, though far from definitive, are much more complete than those for the Whip-poor-will. We present the former herewith, hoping they may minimize future uncertainty and stimulate the accumulation of additional information.

Study Procedures and Methods

Besides numerous notes on population density, species interactions, and territory that we shall publish elsewhere, we made many recordings of vocalizations. In certain cases we saw at least some of the activities of the birds that were associated with particular vocalizations. For this we used 7 × 35 binoculars and a high-powered, sealed-beam flashlight which we frequently, but not always, covered with several layers of red cellophane to make the light less disturbing to the birds.

The importance of standardizing the terminology and description of vocalizations is clearly emphasized by the considerable difficulty that we experienced in trying to tell what our predecessors had really heard in their effort to classify caprimulgid vocalizations. We propose certain standard terms, which we capitalize, for various vocalizations, illustrating all of these with sonograms. Further, we have deposited a tape of these sounds with the Cornell Laboratory of Ornithology, where it will be available for future reference.

We made all of the recordings reproduced here in mid-May, 1965, on a rural road, two miles east and one mile south of Lecompton, Douglas County, Kansas, along the stretch shown in Figures 1 and 2. Occupied by both Chuck-will's-widows and Whip-poor-wills, this stretch of road was a perennial favorite of the former, especially the upper end of the slope shown in Figure 1. Here, during the time of pair-formation, shortly after arrival in spring, and less often later, we found them many times sitting quietly in the gravel road, a few inches to a few feet apart. They sometimes flew up from the road to hawk insects, returning at once. The male often sang, both from the road and from nearby fence posts, as well as from elevated perches well back in the woods. Frequently, they foraged along the clearing made by the road. Later, we shall describe other incidents that occurred here. Also, we shall include additional notes on other individual birds from nearby areas, as well as observations from the literature.

We made our recordings on a Uher 4000 Report-S tape recorder, at 7.5 inches per second, with a fiberglass parabolic reflector and a Shure Model 576 Dynamic, omnidirectional microphone. Our sonograms, all narrow band, were made on a Vibralyzer from the Kay Electric Company.

Vocalizations

Territorial Song

The Territorial Song, or "Chuck-will's-widow," from which the species derives its vernacular name has been presented sonographically and discussed in some detail by various authors. Nevertheless, for completeness, we shall briefly review here what is known about the song, adding a few observations of our own.

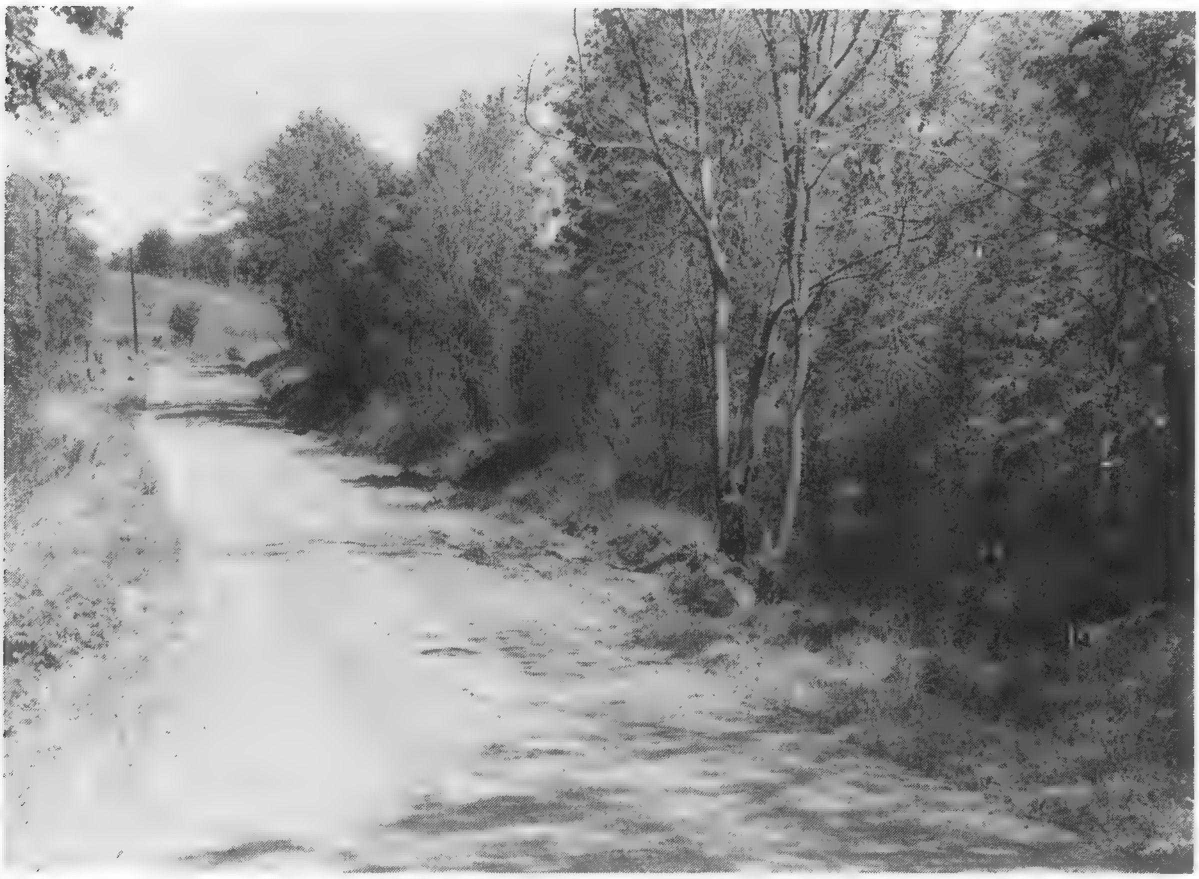


Figure 1. Site of the recordings, looking directly east and slightly uphill. Chuck-will's-widows frequently sat in this stretch of road, especially near the crest of the hill just above the darkest shadows.

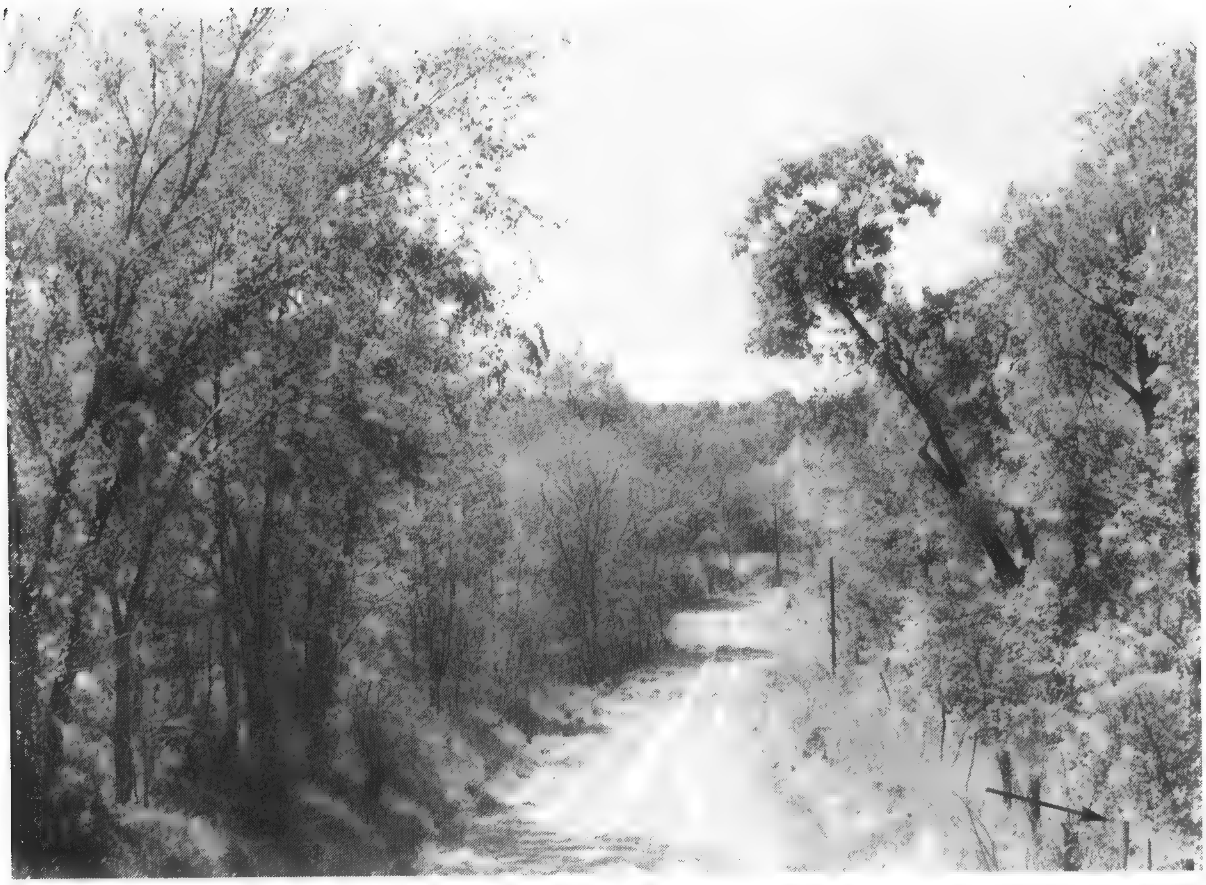


Figure 2. Site of the recordings, looking directly west and slightly downhill. A male Chuck-will's-widow frequently sang from the post indicated by the arrow. The sonogram shown in Figure 5 depicts some other vocalizations uttered from that post. We made the recordings in the heavy shadows on the bank opposite the post.

The song (Figure 3A) is, as Sprunt said (1940:159), "clear-cut, insistent, and sharply enunciated." The version on our sonogram ranges in pitch from 1.0 to 2.75 kilocycles per second (kcs). The exact conformation of the song seems to be variable, probably individually. For example, among other differences, our recording shows a distinct syllable between the *will's* and *widow* notes which is lacking on the several sonograms presented by Davis (1962:87).

Sprunt (1940:158) indicated that songs are given at the rate of about 25 per minute, or at intervals of approximately 2.5 seconds. Harper (1938:11–12) timed frequencies from 16 to 30 songs per minute and attempted to show that song frequency increases with increasing air temperature. We doubt, however, that the possible variables were adequately allowed for by his small sample. Typically, singing is speeded up and then terminated when a male or another female appears — as can be heard on the record of Florida bird songs (Kellogg, 1969).

With unusual exceptions, males sing only at dusk and at night under light conditions which approximate a half moon or brighter. Although we never worked with a light meter, we found we could predict with a high degree of accuracy the time when the males would begin and cease singing. We hope in the future to quantify this relationship, as did Brauner (1952) for the Poor-will (*Phalaenoptilus nuttallii*). This apparent relationship between activity and light intensity may have had a bearing on the success of our almost nightly trips to our study area. It now seems to us that in the years, especially 1965, when the courtship period of the birds coincided with the proper phase of the moon we were able to make many extended observations of the birds' courtship and territorial activities. On the other hand, when the phase of the moon was such that the birds had only the brief period of dusk in which to complete their courtship activities, they did so then and were engaged in egg-laying and incubation, and thus not very conspicuous, by the time the longer moonlighted nights arrived.

The male sings from various "song posts" — trees, snags, fence posts, etc. — throughout his territory, moving regularly from post to post throughout the evening. Except for one male that regularly used a fence post for one of his singing posts, most of the singing birds sat from about six to 35 feet above the ground. One of our observations of a bird at a singing post is pertinent:

> [On 9 May 1965] a Chuck-will's-widow sang off and on, from 7:30 until at least 10:00 p.m. at the curve, sometimes from the road, sometimes from the fence post. We shined him with a sealed beam flashlight, but that did not inhibit his singing. It did reveal that he remained *in situ* for fairly long silent periods, then resuming singing. It also confirmed something we had suspected for some time, namely, that these birds rotate rather regularly on the singing post, thus beaming their song in different directions.

This last observation is important to remember when one attempts to estimate the distance of a singing bird. We think that on a clear night, with no wind, a person with excellent hearing can hear the song up to three-quarters of a mile.

Muted Song

Twice we heard a variation of the Chuck-will's-widow's song, which we call the Muted Song (see Figure 3B). We know of only one reference to this song in the literature and we cannot easily improve on the description given there. Sprunt (1940:160) quoted from a communication from Eugene E. Murphey as follows:

> One observation may be worthy of note, namely, that I have heard the chuck-will's-widow singing as late as September 12 in Edgefield County, S. C. . . . it seemed to me that on this occasion the song was very definitely less vehement and forceful, certainly less frequently reiterated than is the case in spring; in fact, the whole thing seemed to have a querulous and uncertain character. . . .

Our observations support these impressions. On our recording of the Muted Song, the songs are repeated an average of only 8.5 times per minute, being given four to 11 seconds apart. The sonogram shows that the song is not nearly as distinct as the normal song, the initial *chuck* phrase being especially less forceful. The Muted Song is given at a higher pitch and with a greater range of frequencies, 2.0 to 4.5 kcs, than is the normal song.

We heard the Muted Song in the spring, first on 12 May 1965 when we made our sonogram, and again on 5 May 1966 at essentially the same location. Our notes, for 12 May 1965, read as follows:

> We were sitting on the road bank, hidden by shrubs and shadows, when a lone male Chuck-will's-widow appeared on a post across the road, about 35 feet away. This post is one of his favorite singing places but he now indulged in a marvellously clear sequence of varied low-pitched vocalizations, particularly quoks, deep growls, and growls-and-clucks [see our descriptions later]. Shortly after this he retired into the woods and, from the direction in which he had disappeared, we heard a series of very soft, muted songs, about 30 yards from where we were sitting. The sequence lasted several minutes and then all was quiet.

These limited observations do not permit us to speculate as to the significance of the Muted Song; nor is it clear as to which birds are making the sound. It might be a female or a young bird; or it might be a male giving a variation of his normal song in a special situation.

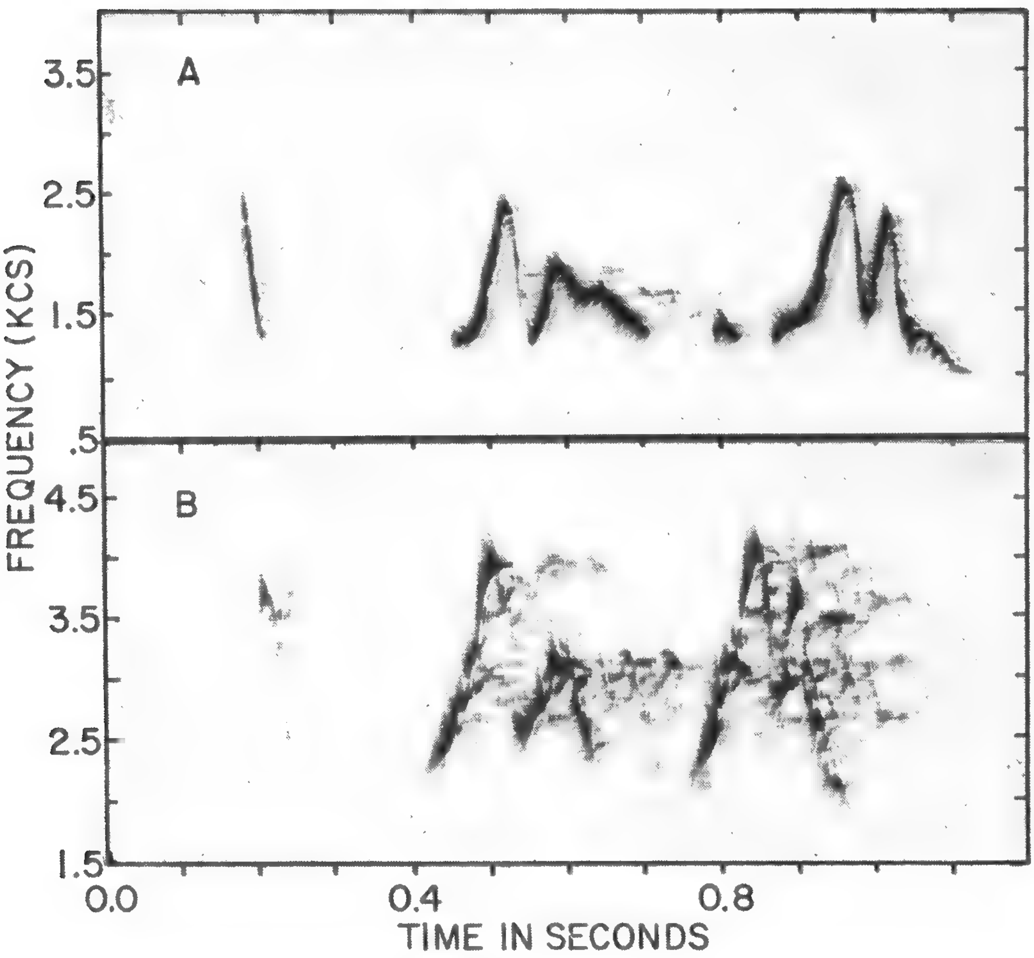


Figure 3. A. Territorial Song of the Chuck-will's-widow. B. Muted Song of the Chuck-will's-widow.

Since the completion of this manuscript, we have moved to a new home in Douglas County, Kansas, which is adjacent to two or more Chuck-will's-widows' territories. We have not yet made any serious effort to observe the birds. However, in the first three weeks of our residency we twice, in mid-June 1971, heard the Muted Song. Both occasions were similar. A male was singing at dusk. He speeded up his song and then abruptly stopped. There was a short pause and then we heard one Muted Song, from the same position as the normal song. These observations suggest to us that the Muted Song may be given more frequently than we earlier thought.

The Growl and Cluck

The most common "non-song" vocalizations of the Chuck-will's-widow are the Growl and the Cluck. Although these two notes are sometimes given separately, they are often given simultaneously (see Figure 4), and the two sounds, as well as the simultaneous version of which they are components, often occur in what appear to be identical contexts.

When they are given together, the timing of the two phrases, as shown in the sonogram, is very precise. We have no recordings of the sounds being given separately, but they seem to be uttered with equal precision. This precision led Jerry Stillwell (see Davis, 1962:78, 88) to call them "time signal" phrases. We have not adopted that term because it refers to the two sounds jointly, and, as we have said, they do not always occur together. The Cluck phrase sounds to us like a glottal *cluck*. The Growl is soft and low in volume; our early field notes often referred to it as a groan. When the two sounds occur together in the Growl-and-Cluck sequence, the Cluck initiates the series, which is uttered at a rate of about two repetitions per second. The effect may be roughly imitated by two people, one softly "growling" *urr-urr-urr* while the other synchronously "clucks" his tongue in rough imitation of a Yellow-billed Cuckoo.

Audubon (1832:274), who apparently was the first to describe the Growl as given by a flying bird, called it a "murmuring noise." Sprunt (1940:159), as do we, described the sound as a "growl." He apparently did not notice the clucking noise although he must have heard it in his extensive experience with the species. At least, he said in response to one correspondent that "I should hardly describe [the growl] as a 'cluck' but it may impress some as such." Fitch (1958:208, and pers. commun.) also noted the Growl in a territorial encounter between two males. He reported the following incidents:

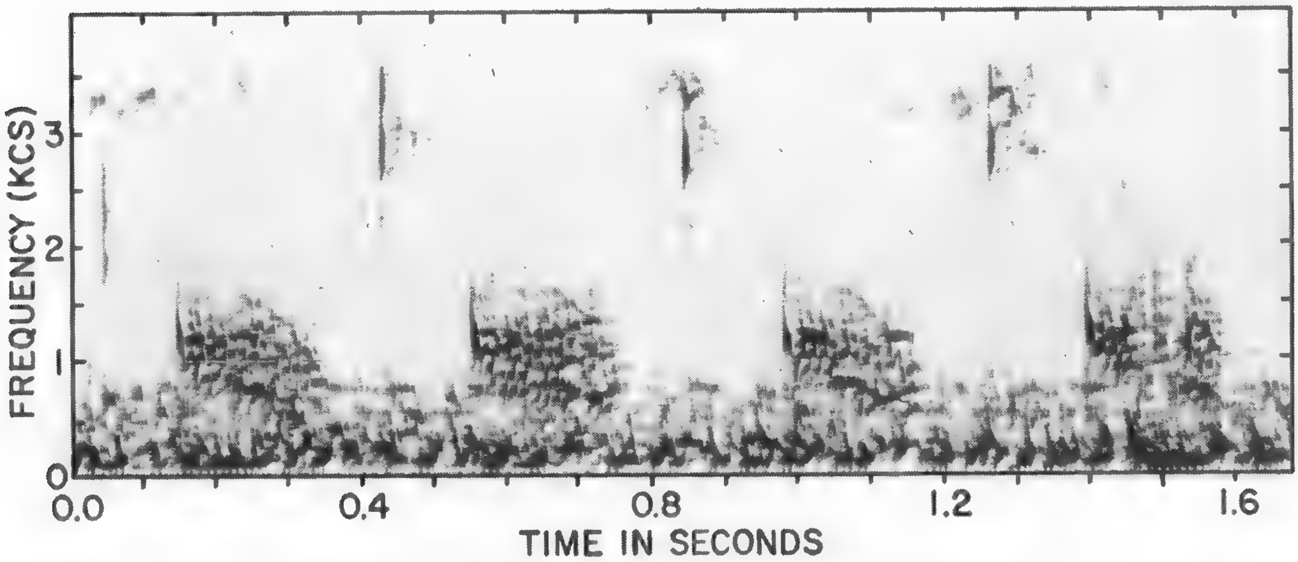


Figure 4. The Growl and Cluck. The Cluck is represented by the narrow, vertical bars; the Growl is represented by the lower and broader bars. The "trash" at the bottom is overall background noise — insects, wind, distant birds, Kansas Turnpike traffic, light aircraft, etc.

> On May 17 one of the [birds] began calling at 7:36 P.M., and soon a second began answering nearby. I approached to within 200 feet and heard a peculiar low growling sound, then saw one in close pursuit of the other in an erratic flight through the trees. They settled and resumed calling only about 50 feet apart and a third was calling on a hillside 150 yards away. Another pursuit, accompanied by the same peculiar growling sounds, was noted on June 6, as one chased a rival from one woodland edge to another, across intervening fields, a distance of some 320 yards. The pursuer quickly returned, and both chuck-will's-widows called, answering each other.

Finally, Harper (1938:12–13) commonly heard a note which he rendered as *quah* or *quuh*. The examples he gave suggest that he was hearing the Growl. He never mentions a clucking sound. A sound he heard from a young bird, described as *grrrr,* may also represent the Growl.

The Cluck may also be the note referred to in the field notes of J. Southgate Y. Hoyt (S. F. Hoyt, 1953) as follows:

> [On 5 May] we heard a bird call . . . very close to us. We waited and soon saw a bird fly from the ground to a tree. Almost at once another bird flew to the ground at the spot where the first had flown up. The first bird doubled back and joined the second on the ground. At this time we heard some fluttering and a slight vocal *chuck*ing. Soon both birds flew off. . . .

Also Hoyt noted:

> [On 17 June] several birds were flying around our yard this evening and giving the *chuck*ing note as they passed near us. On the fence not far from the house we could hear some strange hissing and chucking noises that sounded very much like young birds calling for food.

Our observations suggest to us the following generalizations. The Growl, without the Cluck, is usually given by a flying bird, often by a foraging bird. The simultaneous Growl-and-Cluck is ordinarily given in social situations when two birds, a male and a female or two competing males, are involved. We think it tends to be uttered in an interrupted sequence — three or four repetitions, occasionally on a descending scale, followed by a pause before the next series — when the bird is apparently alone, but continuously when a second bird arrives. We heard the Cluck given alone infrequently. Both sexes make these sounds.

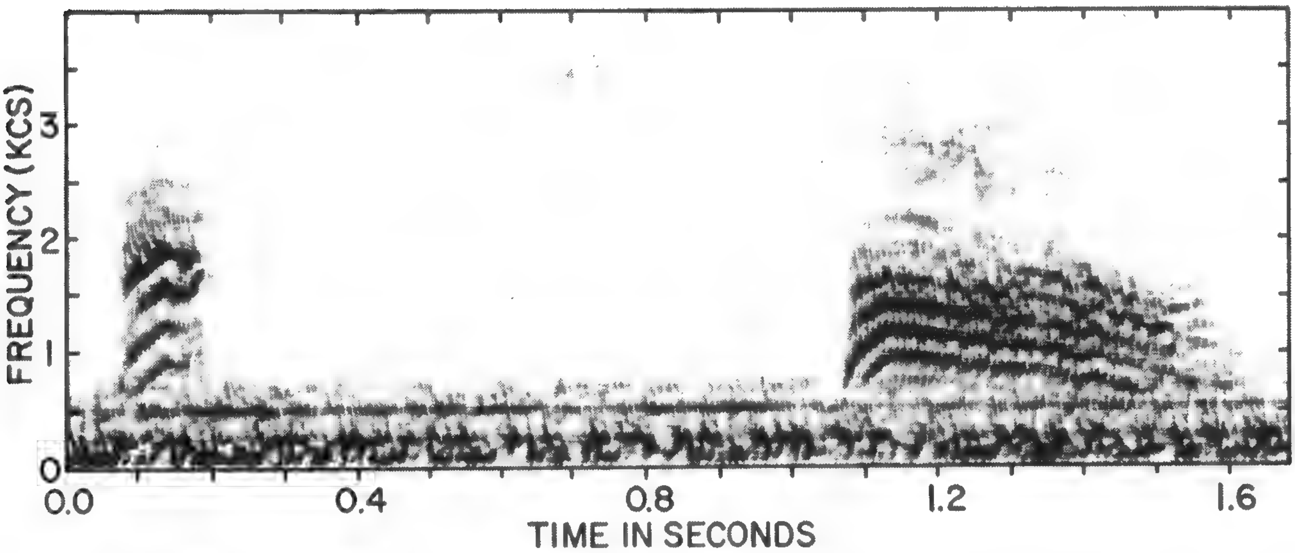


Figure 5. The Quok (left) and Deep Growl (right). We recorded these vocalizations from a male Chuck-will's-widow sitting on the post shown in Figure 2. The background noises, mentioned in the legend of Figure 4, are also present.

A few quotations from our field notes may serve to indicate the variety of situations in which these noises are given.

On 7 June 1963: A Chuck-will's-widow was heard at 8:10 P.M. growling softly. Shortly the growls were interspersed with glottal clucks. Upon entering the grove of low oaks and elms, we flushed the bird from the ground. It flew into nearby trees and immediately began singing about 20 feet up.

On 10 June 1963: At 8:25 P.M., in deep twilight, a Chuck-will's-widow was singing about 30 yards from the road. We recorded about 30 seconds of the song and played it back. Instantly the bird appeared, about 20 feet in the air. It flew straight to us, and in a shallow dive went past about three feet away. The bird circled sharply and alighted in low bushes about seven feet away, where he commenced clucking and growling. We repeated this performance several times. We wanted to record the growls, but the bird would instantly leave off growling and clucking and resume singing when we switched to "record." On one occasion, another bird, presumably the female, passed about 10 feet overhead, growling softly. Once both were growling nearby.

On 7 July 1963: At 8:05 P.M., a female appeared, foraging by circling low over the road and adjacent fields, always in loops and whirls and at altitudes from 5 to 25 feet. She growled softly as she went.

On 10 May 1965: At one point a bird flew overhead growling and clucking. This is the first time we have heard a flying Chuck-will's-widow clucking.

At a different location, a female in the road let us approach on foot to within 15 feet. She was lighted by the headlights. Rhythmically, about every two seconds, she uttered a low growl, each of these making her throat puff out. . . . Later both birds were again in the road, about six inches apart, sitting very quietly. When we were some distance away one flew up a few feet (perhaps hawking insects) then settled down again. We approached to within about 10 feet. The female scooped up a pebble from the road, tossed back her head, and swallowed it [see Jenkinson and Mengel, 1970]. Then the birds flushed. Immediately thereafter there was some growling and very subdued clucking a short distance down the road, followed by a long bout of song.

On 12 May 1965: At 9:20 P.M., a male Chuck-will's-widow appeared in the road a short distance down the hill from us, sat a while, and did a little soft growling. He then did a little "dance," variously growling and clucking throughout [our sonogram is based on this sequence]. His crest feathers were alternately erected and depressed. He shuffled about, making little darts this way and that, waggling his head from side to side, flicking one wing occasionally, jumping into the air a foot or two and coming back. After a little while he went farther down the road and we could tell that a female was with him. There were growls and clucks; it was difficult to see what the birds were doing, but both were moving about on the road. We suspect they may have copulated.

On 4 May 1966: At 11:00 P.M., a Chuck-will's-widow was singing loud and clear in the woods. This bird flew when shined with our spotlight, uttering several glottal clucks, without the growl.

Quok and Deep Growl

The Chuck-will's-widow regularly gives two other vocalizations, the Quok and the Deep Growl (see Figure 5), often in sequence. In fact, we rarely have heard the Deep Growl except in conjunction with the Quok, although the converse is not true. These notes seem to occur under circumstances of higher excitement than the Growl and Cluck.

The Quok sounds to us very much like the flight call of a night heron. Bendire (1895:143) quoted William C. Avery in describing what seems likely to have been this sound as follows:

> When frightened from its nest, or when flying late in the evening, [the bird] utters a harsh note at times, and this resembles, to my ear, the syllable 'baw! baw! baw!' These notes, apparently of displeasure or alarm, are low and cannot be heard at a great distance. . . .

Sprunt (1940:159–160) evidently discussed the same note by quoting Eugene E. Murphey, who said:

> I imagine most field ornithologists are familiar with the froglike croak that the bird makes when flushed, and I am inclined to believe that this note is much more apt to be sounded when the bird has been flushed from the nest.

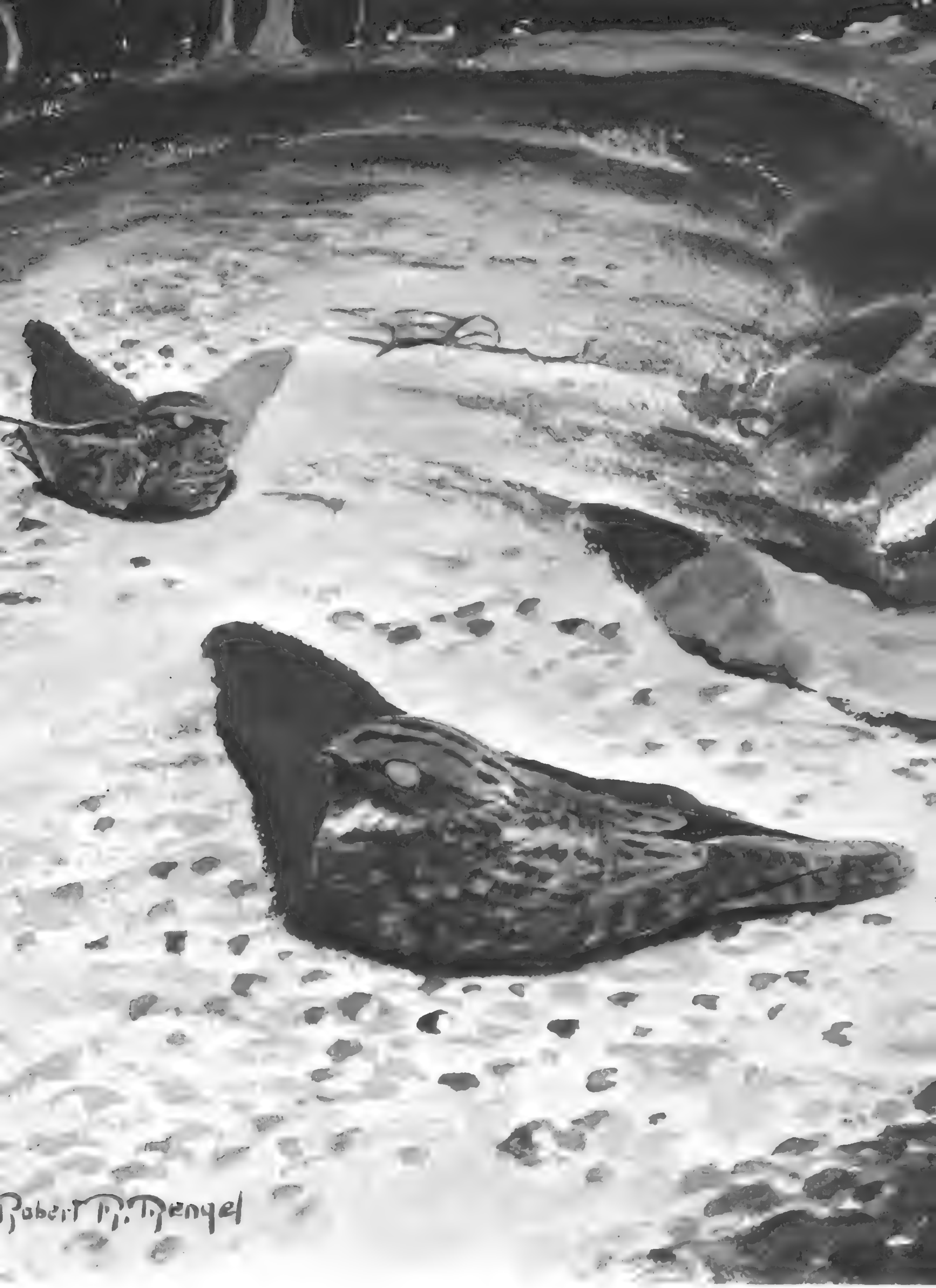
The Deep Growl is a louder, harsher call than the Growl. Its descending quality, seen in the sonogram, is noticeable to the ear. We have found only one description in the literature that seems certainly to refer to this call. Sprunt (1940:160) quoted Herbert L. Stoddard as follows:

> [Chuch-will's-widows] have many gutteral notes of different inflection, . . . a gutteral, low-toned *waugh* given in questioning tones being common. These notes are most frequently uttered when a pair of the birds are together.

Harper (1938:13) described this note as a "bass, resonant *koh, koh.*" He heard this note only rarely, once when another bird was singing nearby.

We have never knowingly flushed a Chuck-will's-widow from its nest, so we have never heard the Quok note in that context. We have, however, heard it many other times under different circumstances, and it seems to us that both the Quok and Deep Growl somehow function in courtship and in the defense of territory. The Quok often serves to notify others of a bird's presence, frequently signaling its arrival in the area.

We often head the Quok given as an "arrival" note, early in the evening, just before the first song. The males apparently utter the note, rather loudly,



Chuck-will's Widow, *Caprimulgus vociferus*. Painting by Robert M. Mengel.

just as they awaken or as they approach or settle at their first song post. Our notes for 6 July 1963, for example, read:

> A Chuck-will's-widow . . . first tuned up at 7:57 P.M., about five minutes after sunset, with several rather loud quok notes, each followed by two or three growls. His first song was at 8:05.

The Quoks and Deep Growls that we heard on 12 May 1965 seemed also to be signals of the bird's arrival at his song post (see the sequence described under Muted Song; our sonogram is based on that sequence). Sprunt and Chamberlain (1949:317) also noted "a very gutteral sound [apparently the Deep Growl] which sometimes precedes the typical call."

We heard the most forceful Quoks when a bird repelled, or attempted to repel, an intruder. A sonogram which we made shows that these notes are identical to the "arrival" notes. We heard these several times, given by males responding to playback of the song, and at least once when birds were involved in a real territorial dispute, as our notes from the night of 11 May indicate:

> A male appeared on a fence post just across the road. He sang normally for a while, then speeded up. We assumed the female had arrived although we could not see her. The male then flew down to the road, some 50 feet away, quoking softly as he did so. In the road he did a little dance—flicking his wings, jumping a foot or more in the air, and jerking his head from side to side, all the while growling and clucking. Once or twice he sang briefly and then flew around just off the road in a little circle. Following him with a red flashlight, we saw that another bird, presumably the female, was on the original post. The male then returned to the road and sat there growling and clucking. Suddenly a third bird flew in without any notice and landed in the road almost in front of us. There was an incredible amount of confusion and much quoking as the two original birds chased the intruder from the area. The three birds passed not more than five feet from our parabola, and the recording we made sounds like one of a flock of small ducks quacking excitedly. There was also one deep growl uttered as the birds flew past. More than one bird, perhaps all three, were making these noises.

On another occasion we heard some of these vocalizations in conjunction with an artificial territorial dispute. On 9 May 1968, we set the mist net across the road and placed a loud speaker, set to play the Chuck-will's-widow's vocalization, under the net. When, shortly after 21:30, we played the first song through the speaker, a male appeared and made several passes at the speaker, flying either around, over, or under the net. Since it was still rather light, we presumed he could easily see the net. During these passes he clapped his wings several times very vigorously. After it was much darker, we tried the same procedure again. This time he made a considerable number of passes, but continued to avoid the net. Finally, alighting on the pole that held the net, with which we had hoped to capture him, he Growled several times, Deep Growled once, and then sang, all the while peering intently toward the speaker. Although the diameter of the pole was only 14 millimeters, he seemed to have no difficulty perching on it. About four or five times he flapped his wings, apparently to help maintain his balance. We did not record how long he remained on the pole, but recall that he stayed at least a minute.

Departure Note

When a Chuck-will's-widow flies off from a sitting position, it gives three or four soft notes which we have called Departure Notes. For some time we called these subdued Quoks. However, when we made a sonogram (Figure 6) of them, we realized that they were not identical to Quoks, but seemed to be intermediate, bearing as much resemblance to Clucks as they did to Quoks. There may be a continuum from Quoking to Clucking, with the Departure Note being halfway between the two sounds.

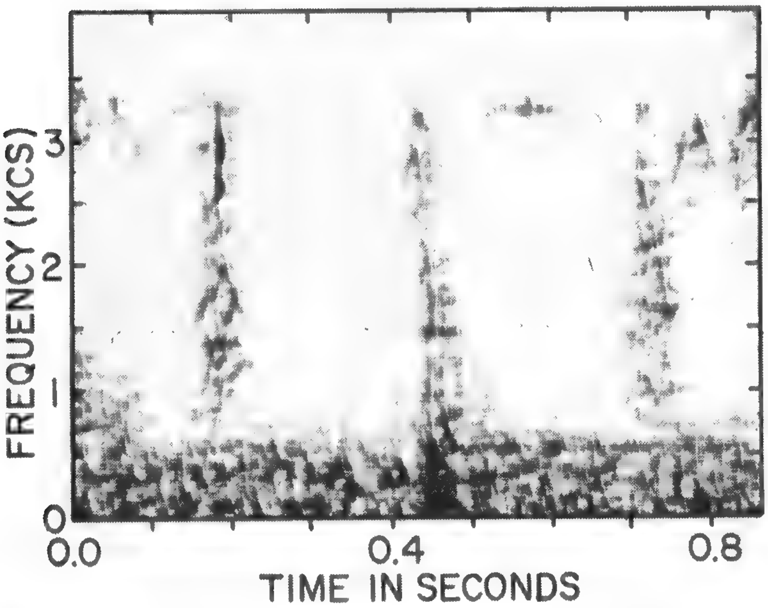


Figure 6. The Departure Note. Notice the resemblance to the Cluck (Figure 4). To the ear, however, the individual Departure Notes also somewhat resemble Quoks (Figure 5). See text for details. The background noise mentioned in the legend of Figure 4 is also present.

Thus, it is often very difficult to tell which of these sounds other investigators have heard and reported. The sequences we quoted earlier, under our description of the Quok, from Bendire and Sprunt, may in fact be describing Departure Notes. Some of the sounds heard by the Hoyts, as described under our account of the Growl and Cluck, may have been Departure Notes. Likewise, the note heard by Holden (1964) may have been either a Departure Note, Cluck, or Quok. Holden reported the following:

> On the evening of 20 April 1963, my wife and I were sitting quietly on our back porch. . . . Suddenly one of these birds alighted on the top of a nearby, small live oak. . . . From this vantage point the bird proceeded to catch insects in the manner of a flycatcher. In a period of ten or fifteen minutes it made, I would estimate, twenty or thirty sallies, always returning to the same tree. . . . During the performance there was no sound from the Chuck-will's-widow except an occasional, barely audible, *chuck.*

Harper (1938:14) seems to have been describing Departure Notes when he reported:

> About noon on April 9, 1933, I flushed two birds together from dead leaves. . . . A very soft note, sounding somewhat like *quoke, quoke,* was uttered as they took flight.

Miscellaneous Sounds

Wing Clapping.—Several workers, including ourselves, have heard or seen Chuck-will's-widows Wing Clapping. This is a common behavior of the European Nightjar (*Caprimulgus europaeus*) but it has not yet been precisely described in the literature for any North American caprimulgid. Mengel *et al.* (1972) will soon publish a discussion of this behavior in the Chuck-will's-widow. Although it is not a vocalization, we mention it here because it is a means of communication and was given in one of the behavioral sequences described above. It probably functions in the maintenance of territory.

Hissing. — When a Chuck-will's-widow is captured by a person, or, presumably, by a predator, it opens its large mouth fully and utters a loud hissing noise, an action that may help in effecting its release. Even after we had handled several of the birds and anticipated the behavior, it startled us. We think the birds may be mimicking a snake. Sibley (1955) gave many examples of birds, all hole-nesting species, which hiss and gape in a "snake display." He suggested (p. 130) that the occurrence of such a display in hole-nesting species is correlated with the fact that they have no avenue of escape from a predator entering their nest opening. Chuck-will's-widows nest on the ground but have been reported as roosting in natural cavities (Sprunt, 1940:153) or in hollow logs (Audubon, 1832:273–274). In fact, Audubon reported:

> When surprised in such situations, instead of trying to effect their escape by flying out, they retire backwards to the farthest corners, ruffle all the feathers of their body, open their mouth to its full extent, and utter a hissing kind of murmur, not unlike that of some snakes.

The hissing sound may be similar to that heard by the Hoyts and described under our section on the Growl and Cluck, possibly given by begging young birds.

We think that Audubon's report (1832:276) of Chuck-will's-widows regularly hissing and gaping at snakes needs verification.

Cuckoo Note. — On one occasion we heard an unusual note, given three times, which we think was made by a Chuck-will's-widow. On 11 May 1965, just after a male and female had repelled an intruding bird (as we described under Quok and Deep Growl), one of the birds apparently returned and landed in the woods just across the road from us. In any event, we heard three sounds from that area which we can associate with no other animal. Immediately thereafter, a male Chuck-will's-widow flew in from where we thought the sound had originated. He landed in the road and began to sing a normal song.

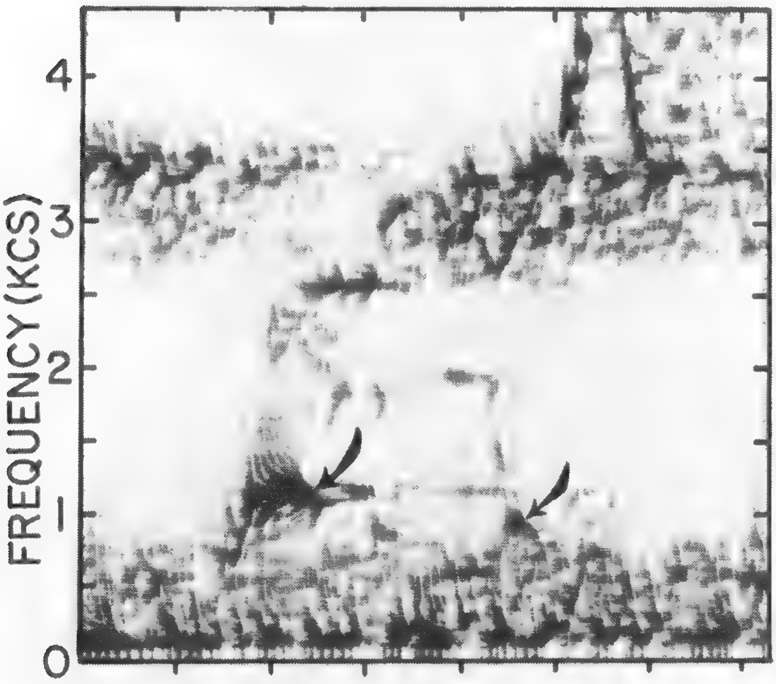


Figure 7. The strange "cuckoo note." Arrows indicate the two portions of this vocalization. In addition to the "cuckoo note," this sonogram includes, at higher frequencies, part of a Whip-poor-will's song, and, at low frequencies, the background noises mentioned in the legend of Figure 4.

The note (Figure 7) sounded to us like the "cuckoo" made by a cuckoo clock, but more liquid and melodious. The notes were separated by four or five seconds each. We recorded one of these, and present it here, even though it is somewhat flawed by background noises.

A Final Perplexity. — For some time we were puzzled by a sound described by Sprunt and Chamberlain (1949:317). They quoted from a manuscript by Edward von S. Dingle, in which that author reported having heard a "sing-song 'konk, konk, konk' repeated as many as 25 or 30 times." This description did not seem to correspond with any sound that we had heard from these birds. We wrote to Mr. Dingle for further information, and his reply to us on 5 October 1970 contained the following notes: "I have never heard any note given in flight except the croaking 'quak' when the bird is flushed." This would be either the Quok or Departure Note. Further: "One has to be very near the bird to hear the soft, murmuring call." This would be the Growl. And: "The nearest approach of putting the 'konk' call into words seems to me the use of this word; there is a decided quality of plucking the strings of one of the larger fiddles." On the basis of these remarks, we have concluded that the "konk" note is probably the Deep Growl. First, the birds rather regularly make the Deep Growl, and it would be remarkable if Dingle had not heard it. None of his other comments are referable to that vocalization. Also, the Deep Growl sounds very much indeed like a note from the bass fiddle. We were not happy with Dingle's choice of the word "konk" to describe the sound, however, until we realized that a difference in our dialects might account for his interpretation. The word "konk" pronounced by a Kansan would not describe the Deep Growl, but as pronounced by a person from South Carolina it might. We were surprised that Dingle heard this note given 25 or 30 times; we never heard the Deep Growl being repeated more than two or three times.

Summary

From 1963 through 1968, we made extensive observations on the Chuck-will's-widow (*Caprimulgus carolinensis*) in Douglas County, Kansas. We recorded what may be all of the vocalizations of the species, and here name, discuss, and present sonograms of them. The "Chuck-will's-widow," or Territorial Song, is related to courtship and territoriality. A Muted Song, heard only rarely, has a yet unknown function. Growls and Clucks are regularly given separately or simultaneously, both by flying birds, often when foraging, and in social situations between two males or a male and a female. Quoks and Deep Growls are heard less often and are given in territorial situations. These sounds often signal a bird's arrival at his singing post. Also we heard them being given very forcefully when a male repelled another bird from his territory. A Departure Note is regularly given three or four times as a bird flies off from a sitting position. Wing Clapping, hissing, and an unusual "cuckoo note" are also part of the repertoire of sounds of these birds.

Acknowledgments

We are especially indebted to Joyce L. Wildenthal, who helped us in our earliest recording ventures, and to William E. Duellman, who kindly loaned us his sonographic equipment and instructed us in its use. We thank Edward von S. Dingle for sharing with us his notes on the Chuck-will's-widow. Thomas H. Swearingen helped prepare our illustrations and Dorothy Craig was most efficient in typing our manuscript.

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AN ECOLOGICAL STUDY OF THE BIRDS OF THE LOWLAND PINE SAVANNA AND ADJACENT RAIN FOREST IN NORTHEASTERN NICARAGUA

Thomas R. Howell

This study concerns the avifauna in an extensive area of pine savanna that lies on the lowlands of the Caribbean slope in northeastern Nicaragua and eastern Honduras. This distinctive habitat, which supports only one species of pine, *Pinus caribaea,* is completely isolated by many miles of broad-leafed tropical rain forest or moist forest from the pine "ridges" of British Honduras and the highland pine forests of Honduras and Nicaragua (Figure 1).

General Ecology of the Pine Savanna

To summarize briefly from Parsons (1955), Radley (1960), Taylor (1963), and Munro (1966), who discussed the geography and some aspects of the ecology: the lowland pine savanna extends over approximately 9,200 square kilometers (calculated from a map in Radley) to 10,000 sq km (Munro, 1966) in Nicaragua, and about 6,600 sq km (from map in Monroe, 1968) in Honduras. Pines and grasslands occupy the greater part of the flat or gently undulating terrain that is generally less than 200 meters above sea level. The broad-leafed forest extends into the savanna along numerous watercourses and forms islands in low-lying areas throughout. I estimate that the incursions of broad-leafed forest occupy about one-fourth of the region; Parsons (1955) estimated one-third.

The savanna region corresponds fairly closely to an area of yellow-red latosols and hydromorphic soils associated with Pleistocene sediments; Radley (1960) considered it Pliocene; I have no precise dating of sediments. Within the area, the pines usually occupy expanses of very poor soil with little or no humus and only a relatively thin topsoil of sand, gravel, and clay overlying a deep bed of heavy, impermeable clay. The broad-leafed forests grow primarily in alluvial soils but can and do invade the poorer soils usually occupied by pines, and pines will grow in the richer soils if not shaded out in the seedling stage.

Frequently the boundaries between the pine savanna and rain forest are abrupt (Figure 2), but sometimes the pines and broad-leafed trees intermingle in a narrow zone. There are also extensive grasslands where trees and shrubs are sparse or lacking altogether.

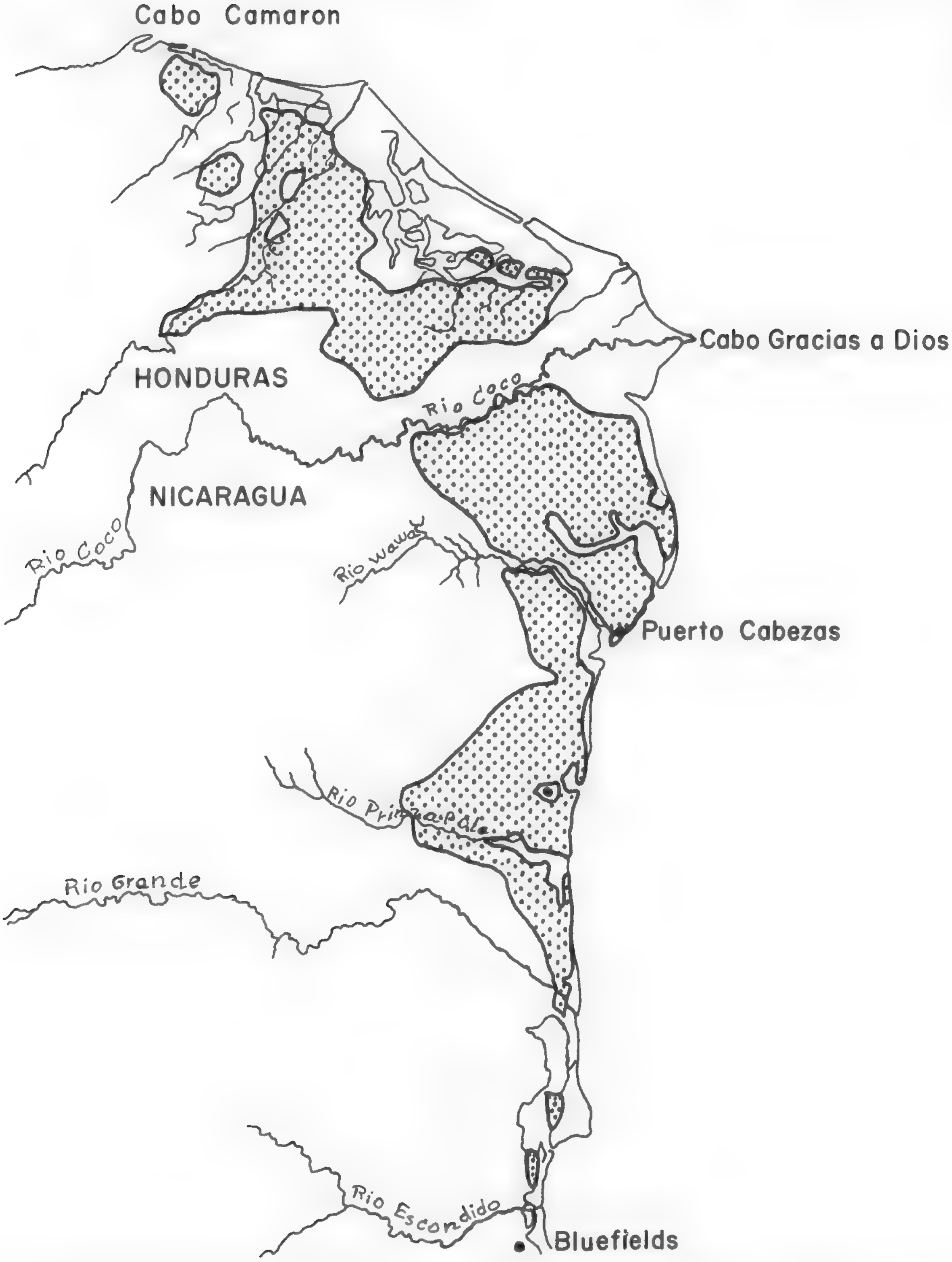


Figure 1. Eastern Honduras and Nicaragua in Central America showing the extent of lowland pine savanna (stippled area).

The humid, tropical climate has an average daily temperature of about 25° Centigrade and the minimum temperature is rarely below 20°C. The annual rainfall of 2,600 to 3,500 millimeters makes this savanna one of the wettest in the world. Talbot (1964) gives 1,270–1,524 mm for Africa, and Blydenstein (1967) records 1,700 to 2,000 mm for most of the llanos of Colombia "... increasing sharply near the base of the mountains to over 4,000 mm at Villavicencio." In the Nicaraguan pine savanna, a relatively dry season starts in February and extends through April, with March and April usually the driest months. Average rainfall records, compiled at Puerto Cabezas on the Caribbean coast, for the two dry months are: 1927–1950, March, 61.2 mm; April, 50 mm (Parsons, 1955); 1955–1959, March, 36.8 mm with extremes of 1.3–72.1 mm; April, 41.1 mm with extremes of 10.2–108.7 mm (Radley, 1960).

The precipitation varies locally so that, even in the dry season, rain falls over some part of the savanna almost every day. The areas where broad-leafed forest and pine savanna are contiguous probably receive the same amount of rain, but the soil penetration, run-off, and evaporation rates must differ considerably in the two habitats.

Even in March and April, numerous creeks flow throughout the savanna, and some small ponds appear to be permanent. However, most of the area of pines and grass dries out after a few sunny days, and grass fires, once started, spread rapidly.

The Nicaraguan pine savanna has been logged continuously since the 1920's, and almost no large pines remain in easily accessible regions. A good stand of pines may include trees up to 25 meters high; the rings of the larger felled trees indicate an age of about 70 or 80 years.

The age of the pine savanna is unknown and somewhat controversial. Parsons, Radley, Taylor, and Munro, as well as Denevan (1961) and Johannessen (1963), agree that the pine savannas owe their continued existence to periodic burning. The unsettled questions are whether the savannas originated through the clearing and burning of the broad-leafed forest by man, and if so, when the process began, or whether the savannas are the results of blowdowns by hurricanes, followed by lightning-started fires, possibly before the occupation of the region by man. Certainly, within historic times, man-made fires have maintained or extended the area of the savanna by destroying the encroaching broad-leafed seedlings and leaving the larger pines that are able to survive repeated burnings of the grassy understory (Figure 3).

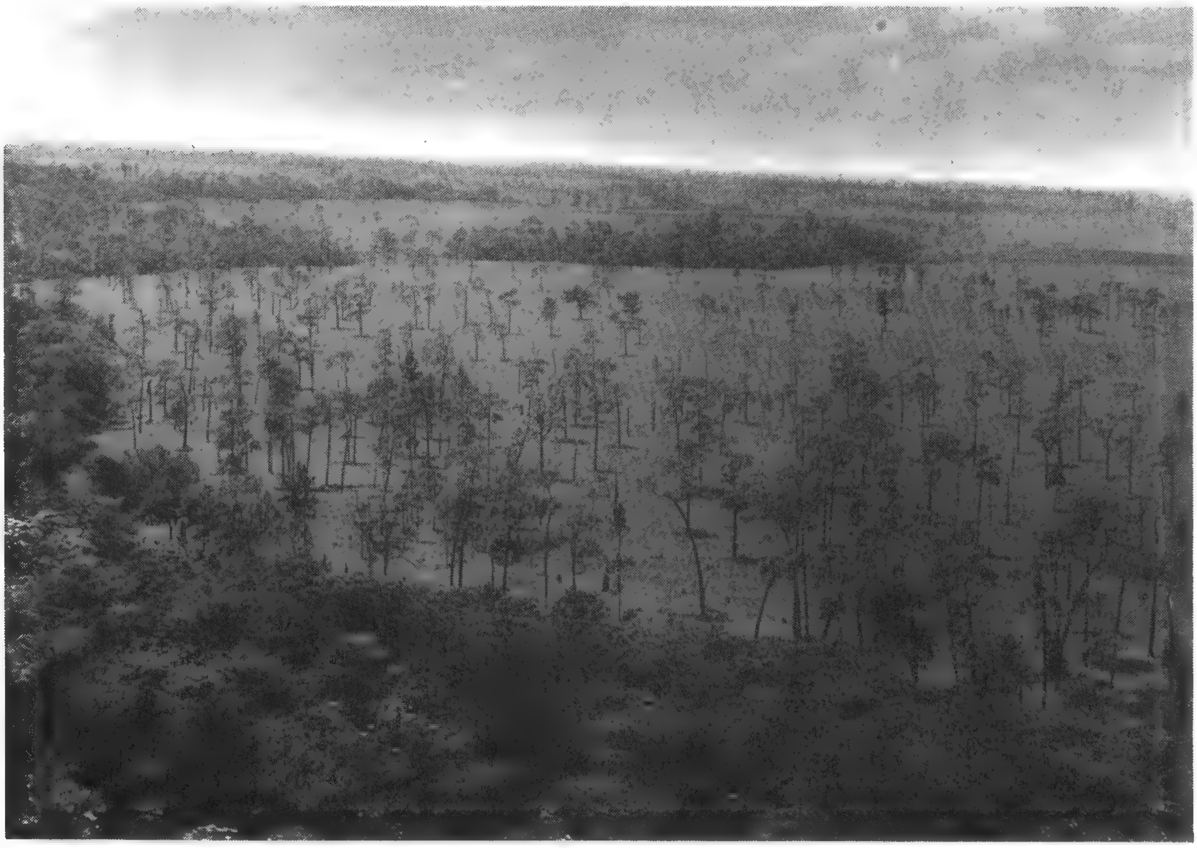


Figure 2. Rain forest-pine savanna interface, northeastern Nicaragua. Note the abrupt boundary here between the pine savanna and the rain forest (bottom of photograph).

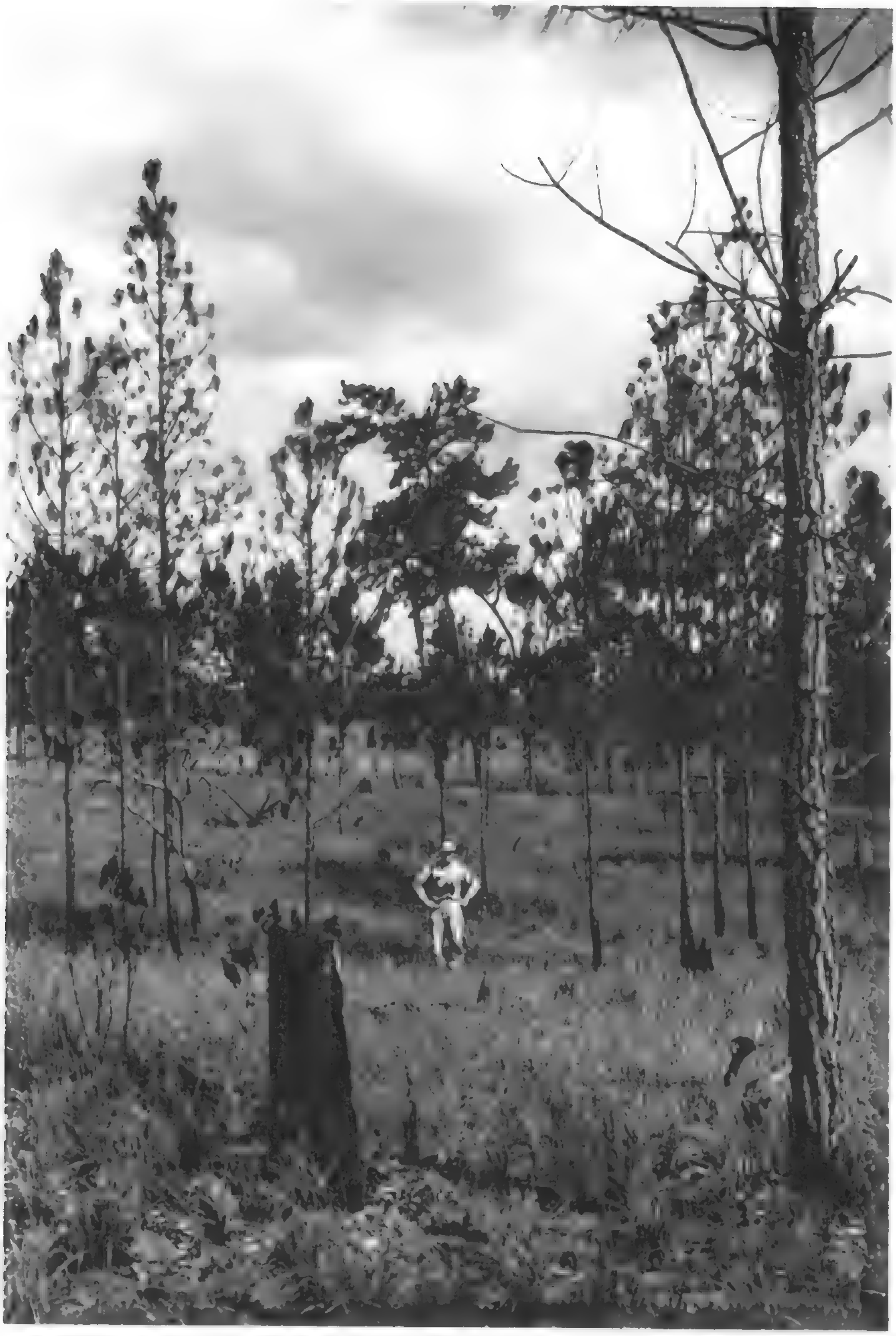


Figure 3. Recently burned portion of pine savanna, showing damage to small pine seedlings and lower branches (but undamaged crowns) of larger trees. Note rapid regrowth of grasses. Man-made fires are important in maintaining the savanna and preventing encroachment of broad-leafed trees.

Ornithological Interest of the Pine Savanna

The pine savanna is of ornithological interest because: (1) it includes the southern limit of naturally occurring pines in the Western Hemisphere; (2) it includes the southern limit of the ranges of several pine-adapted species of birds, such as the Grace's Warbler (*Dendroica graciae*), Red Crossbill (*Loxia curvirostra*), and Chipping Sparrow (*Spizella passerina*); and (3) its isolation has led to the differentiation of several endemic subspecies of birds (Howell, 1965).

The region is of ecological interest because the pine forest is a very ancient and extensive vegetational association in the northern hemisphere and constitutes a distinctive temperate-zone habitat to which many organisms, including birds, are specially adapted. Although pines have penetrated tropical latitudes throughout the world, in the New World tropics they usually appear in montane regions, such as the Mexican plateau and the Central American highlands, where the climate tends toward temperate. The Nicaraguan-Honduran savanna, however, lies in lowlands between 12°10′ and 16° N Lat., where the climate and general environmental conditions are entirely suitable for the well developed tropical rain forest that surrounds and interdigitates with it. In effect, the lowland pine savanna constitutes an irregular "island" of temperate-zone habitat set down in humid tropical surroundings.

The transition from a lush tropical forest with an abundance of cotingas, manakins, and antbirds to the pine savanna with a scattering of Common Meadowlarks (*Sturnella magna*), Common Bluebirds (*Sialia sialis*), and Chipping Sparrows is startling. This juxtaposition of primarily tropical and primarily temperate avifaunas offers a rare opportunity for a comparative study of the abundance, diversity, and ecologically relevant behavior of the resident birds under identical macroenvironmental conditions. The fact that the same day length, seasonal change in climate, elevation above sea level, and the basic soil conditions exist in both the savanna and broad-leafed forest narrows the range of environmental parameters that the investigators must consider in accounting for the differences in the avifaunas of the respective habitats.

Aims of the Study

The principal questions that I have considered are:

(1) What are the precise qualitative and quantitative differences between the avifaunas of measured areas of tropical pine savanna and adjacent broad-leafed forest?

(2) Within the tropical savanna, what are the differences between the bird populations in areas of pine with little understory and few seedlings, areas of pine with abundant seedlings of different heights, and treeless areas of grasses, sedges, and a few shrubs?

(3) Are the differences in bird populations in the various habitats predictable on the basis of the different foliage profiles, as proposed by MacArthur and MacArthur (1961)?

(4) How do the bird populations of the tropical habitat compare, in numbers of species and numbers of individuals, with bird populations in temperate-zone habitats?

(5) Does competition between bird species influence their restriction to different habitats?

(6) Considering the composition of the avifaunas of the different habitats, what may one infer about competition, niche size and degree of niche overlap, and inter- and intraspecific partitioning of resources?

(7) How do the proportions of non-passerines to passerines and suboscines to oscines differ in the two habitats and how may one interpret the differences?

(8) What is the ecological effect of wintering North American migrants on the resident birds in both habitats?

(9) What historical factors may have been responsible for the differences in the avifaunas of the two habitats?

(10) What relevance do the answers to these questions have to the subject of latitudinal gradients in bird species diversity?

Methods

I visited the savanna region from 2 to 4 February 1955, 22 January to 20 February 1962, 16 January to 1 February 1963, 11 to 27 August 1965, 10 to 26 March 1966, 18 November to 1 December 1966, and 15 to 30 April 1967. Thus, I was present in both the wet and dry seasons, when the migrants were there from the north, and when breeding birds not resident the year round were present.

I studied intensively three areas—two in the pine savanna and one in the rain forest—and investigated less thoroughly two other savanna areas—one with a sparse growth of pines and one with grass and no trees.

For measuring the foliage characteristics and the bird species diversity of the different areas, I used the method described by MacArthur and MacArthur (1961). This permits direct comparison of my data from Nicaragua with the results obtained by MacArthur and his co-workers in temperate North America and in Panama (MacArthur *et al.*, 1962; MacArthur, 1964; MacArthur *et al.*, 1966). Appendix 1 presents a brief resumé of this method and some minor modifications that we used to suit local conditions.

From measurements of vegetation density at different vertical levels, MacArthur and MacArthur (1961) calculated Foliage Height Diversity (FHD) for each of their study plots. From censuses of breeding birds in these plots, they calculated Bird Species Diversity (BSD) using the same equation as for FHD (see Appendix 1). When they plotted FHD against BSD for each of their plots, the results yielded a series of points that clustered about a straight line. A consideration of plant species diversity in relation to bird species diversity did not reduce the scatter of points or provide a better fit by a straight line. The authors concluded that BSD could be predicted, at least in certain temperate zone habitats, from FHD alone without considering the species composition of the vegetation. Their equation is $\text{BSD} = 2.01\ \text{FHD} + .46$. However, MacArthur (1964) pointed out that in the case of certain habitats and with some birds of specialized food habits, the proposed relationship between FHD and BSD might not hold. In a later section, I present measurements of FHD and BSD for the Nicaraguan pine savanna and rain forest areas, comparing them to temperate zone areas and discussing their predictability.

Antonio Molina R. identified many of the plants in the savanna area in the field, and we collected others for later study at the herbarium of the University of California, Los Angeles. Appendix II groups qualitatively the most conspicuous plants of the savanna study areas and includes a brief description of their appearance and importance to the bird fauna.

Description of Study Areas

We made quantitative measurements of vegetation density in plots designated as Pine Savanna Area 1, Pine Savanna Area 2, and Rain Forest Area, and calculated the FHD for each (Figure 4). These plots were all close together in terms of absolute distance and elevation. I have located each in relation to Waspam, about 75 miles or 120 km northwest of Puerto Cabezas in the Comarca de El Cabo. All had the same elevation, 65 m, except the Rain Forest Area which was 130 m. The Grassland and Rain Forest Areas are the same distance from Waspam though not contiguous; both lie along a curved road, approximately 14 miles or 22 km south southwest of Waspam, with the difference in compass directions too slight for notation.

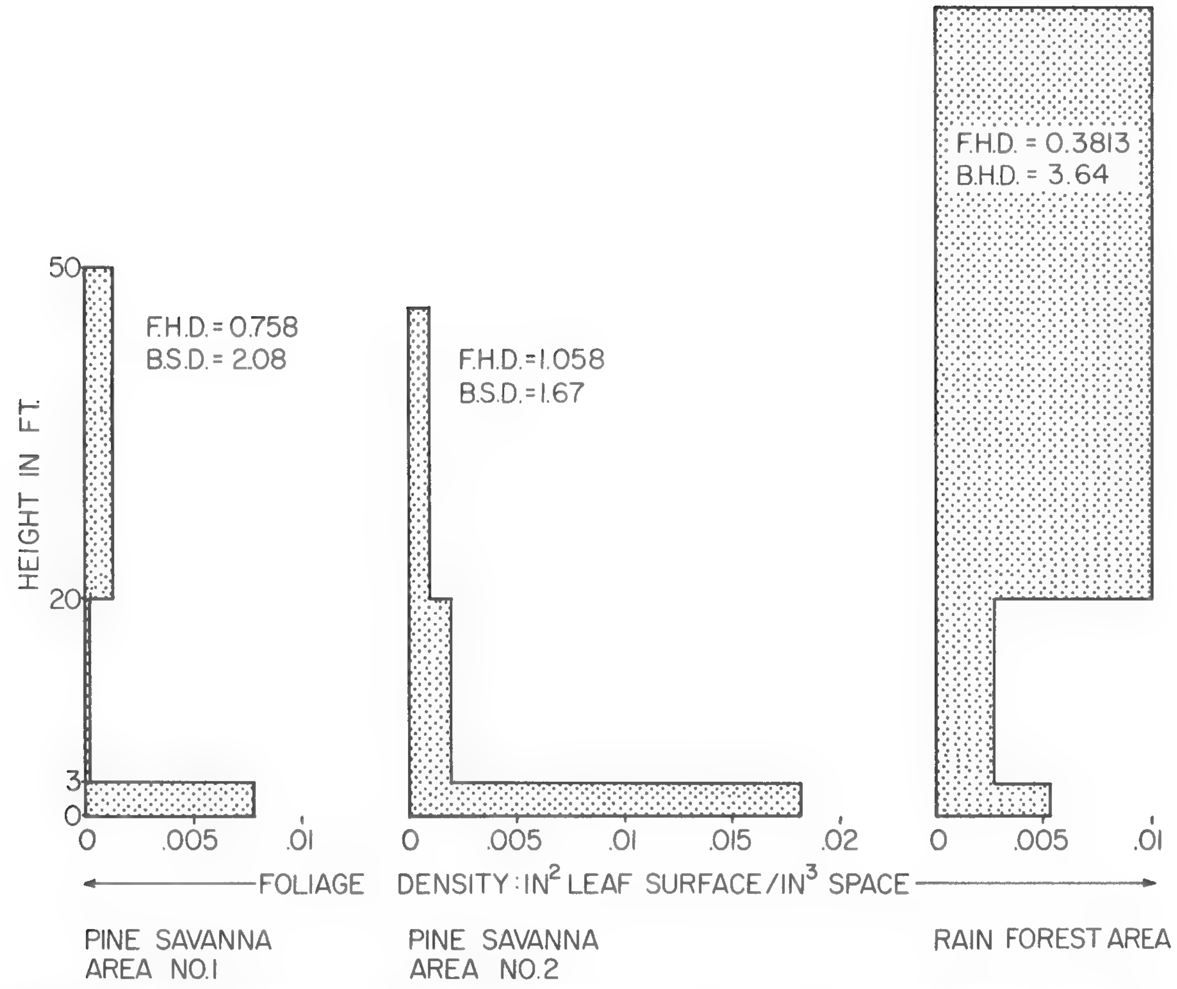


Figure 4. Foliage profiles, foliage height diversity (FHD), and bird species diversity (BSD) for Pine Savanna Areas Nos. 1 and 2 and the Rain Forest Area. See text for explanation.

Pine Savanna Area 1

Leicus Creek, 22.5 km southwest of Waspam; 25 acres, 348 by 348 yards.

Characteristics (Figure 5): Pine trees irregularly spaced, moderately dense; average height of 27 trees above 25 feet, chosen at random, 50.2 ft, extremes 27 to 71 ft; seedling pines and large shrubs sparse; dense ground cover of grasses and sedges; no streams or permanent standing water, but some low lying wet areas; permanent streams within 100 m; dirt road, rarely used, running through area near eastern edge.

Most conspicuous plants: Trees—*Pinus caribaea,* throughout; *Curatella americana,* scarce. Shrubs—*Byrsonima crassifolia,* throughout; *Miconia lundelli,* throughout; *M. albidea,* throughout, but less common than *M. lundelli.* Herbs—*Tibouchina belizensis,* mostly in lower areas with slow drainage; *Clidemia rubra,* throughout; *Polygala* sp., throughout; *Diodia frutescens,* throughout; *Borreria suaveolens,* throughout. Grasses and sedges—*Paspalum humboldtianum,* throughout; *Panicum* sp., throughout; *Aristida* sp., throughout; *Andropogon* sp., edges of road, scarce; *Hypolytrum schraderianum,* throughout; *Bulbostylus paradoxa,* throughout; *Rhynchospora barbata,* throughout; *Fimbristylis* sp., throughout. Arboreal plants—*Psittacanthus mayanus,* fairly common; *Aechmea bracteata,* fairly common; *Tillandsia* sp., abundant. Ferns—*Blechnum* sp., in low-lying wet places.

Pine Savanna Area 2

Located 15.3 km south southwest of Waspam; approximately 15 acres of a square 345 by 345 yds, of which about 10 acres was burned in 1965 and lacked trees or shrubs; the burned section, one corner of the square, was excluded from study area.

Characteristics (Figure 6): Pine trees irregularly spaced, moderately dense; average height of 25 trees above 25 ft chosen at random, 46.3 ft, extremes 31.5 to 68 ft; seedling pines numerous, often dense; large shrubs numerous in some sections; ground cover of grasses and sedges denser and higher than in Area 1; standing water in low-lying areas; frequently used dirt road running through northern edge.

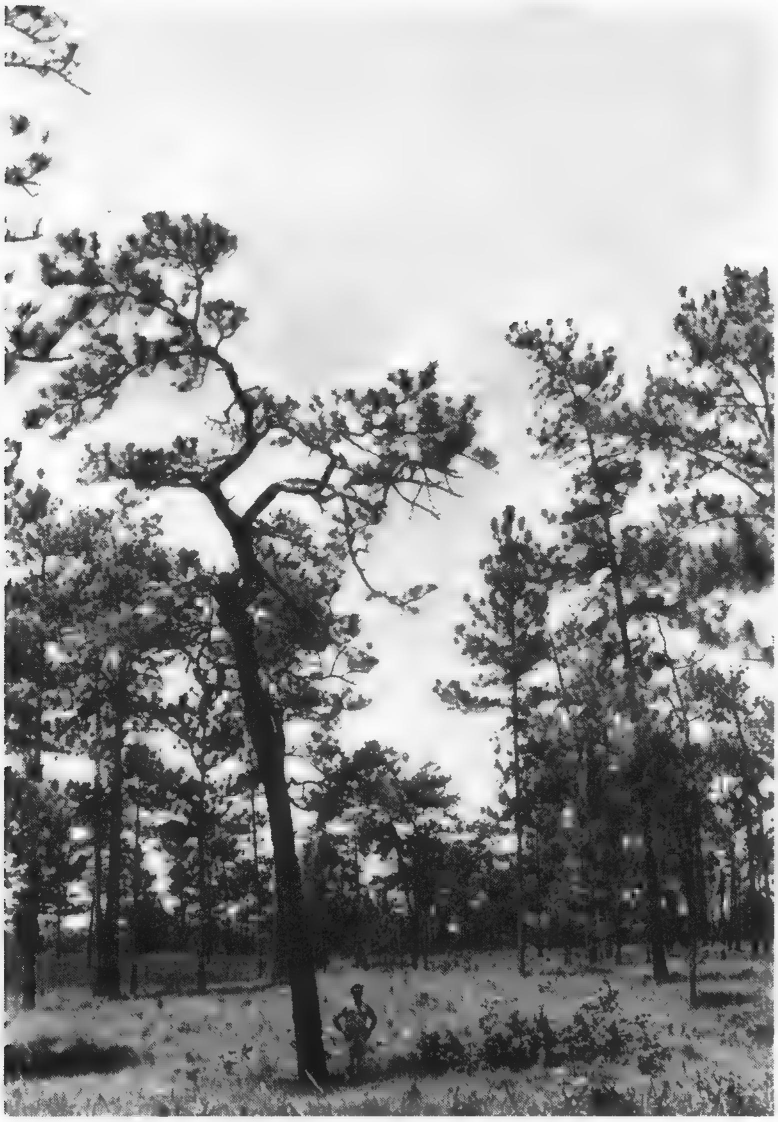


Figure 5. Pine Savanna Area No. 1.

Most conspicuous plants: As in Area 1 with the following exceptions: Shrubs—in northern part of area, *Miconia scorpioides, M. impetularis, Palicourea guineense,* and a few young *Xylopia frutescens* in small numbers; *Tibouchina belizensis* in dense stands in the same area; all stands were between 1.5 and 2 m high. Grasses and sedges—*Paspalum humboldtianum* much more luxuriant than in Area No. 1; the smaller plants of the ground cover were fewer.

Pine Savanna Area 3

Located 20 km southwest of Waspam; 25 acres, irregular pentagon, longest side 350 yds.

Characteristics (Figure 7): Similar to Savanna Area 1, but trees and shrubs sparser and ground cover of grasses and sedges lower and less dense; permanent small stream, bordered with dense stands of cane grass (*Tripsacum* sp.), winding through area; a few low-lying spots that seemed permanently wet support dense stands of *Tripsacum, Tibouchina belizensis,* and large sword ferns; a few clumps of *Sabal* palmetto; gravel road, frequently used, outside western edge. No measurements of tree heights or vegetation density.

Grassland

Located 25 km south southwest of Waspam; 5 acres, 155 by 155 yds.

Characteristics (Figure 8): Dense grass and sedges with few shrubs and pine seedlings usually no higher than the grass; average height of dense grass, measured at 15 random points, 1.85 ft; maximum height of sparse blades, about 3 ft; one dead weathered pine about 15 m high in center; conditions varying from low cover and bare ground on dry soil to taller denser cover and some standing water in low areas; surrounding area largely grassy, with sparse growth of small pines near two of the sides.

Most conspicuous plants: Grasses and sedges as in Pine Savanna Area 1; *Andropogon* in a few small clumps; *Byrsonima crassifolia* and *Tibouchina belizensis* sparsely distributed; a few pine seedlings about 1 m high.

Rain Forest Area

Located about 25 km south southwest of Waspam, elevation 130 m; approximately 10 acres, irregular quadrilateral with longest side 300 yds and shortest, 157 yds.

Characteristics (Figures 9 and 10): Many species of broad-leafed hardwood trees; numerous epiphytes, philodendrons, and lianas; bamboo and *Heliconia* abundant at edges and in more open areas in forest; several small permanent streams winding through; average height of 10 trees over 25 ft high, selected at random, 74.3 ft, extremes 36 to 142 ft; understory of seedlings, herbs, and small palms (some thorny); terrain slightly contoured, maximum difference in elevation about 10 m; not primeval; evidence of small amount of selective logging probably within past five years; numerous second-growth indicator species; trail along one edge with clearing beyond.

Most conspicuous plants: Species composition greatly mixed; most trees not identified; see Taylor (1963) for characteristic lowland evergreen trees found in the rain forest on the Caribbean slope in Nicaragua.

Avifauna of the Pine Savanna

A relatively small number of bird species use the savanna habitat. Table 1 lists 56 species although we did not record all of these in the study areas. The list does not include water birds and waders that may occur in and out of the savanna, nor the spring and fall transients that are present only briefly, nor all the species ever recorded in or over the savanna. Rather, the list includes all species that use the characteristic features of the savanna in some ecologically important way, or combination of ways—i.e., foraging, feeding, resting, nesting—with at least some regularity. Because equivocal cases are inevitable, I have provided some explanatory footnotes in Table 1. The categories are:

Permanent residents—resident species whose presence in this general region depends on the presence of the savanna. These birds carry on most or all of their activities in the savanna and are absent from the broad-leafed forest.

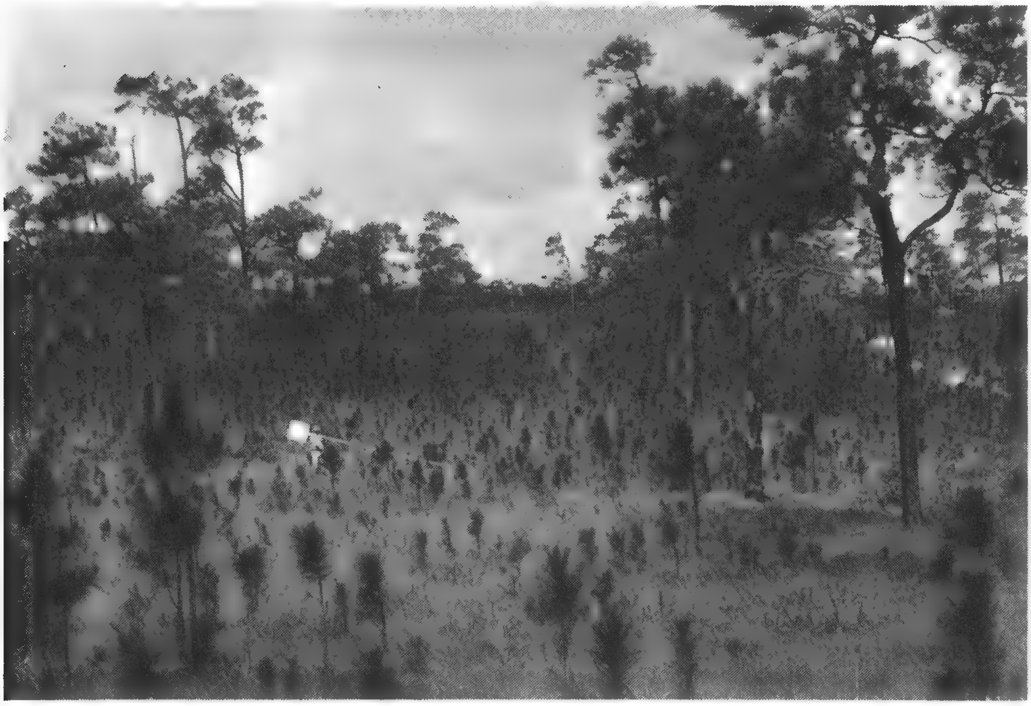


Figure 6. Pine Savanna Area No. 2. Note the abundance of seedlings, and the white board and poles used for foliage measurements.

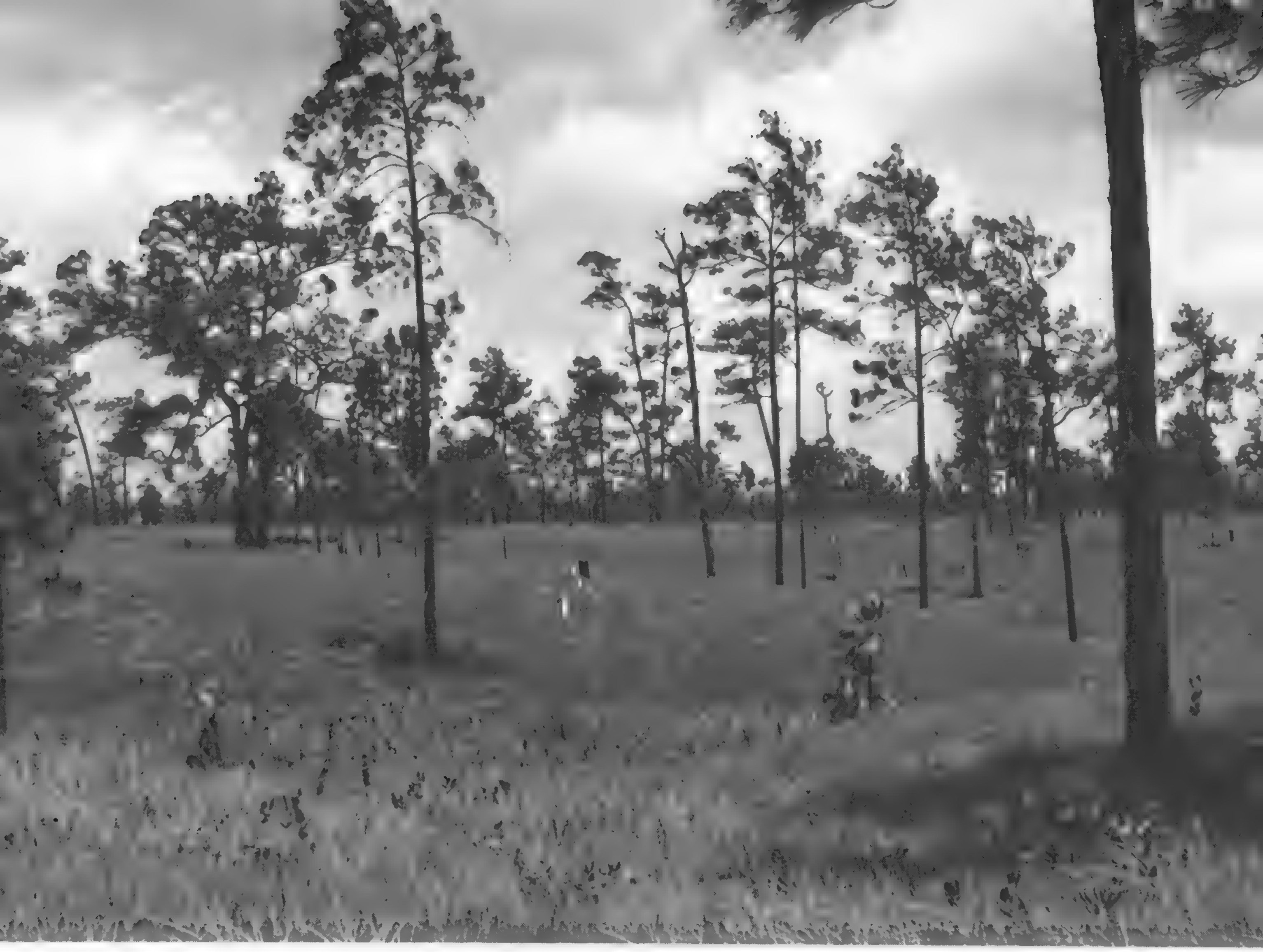
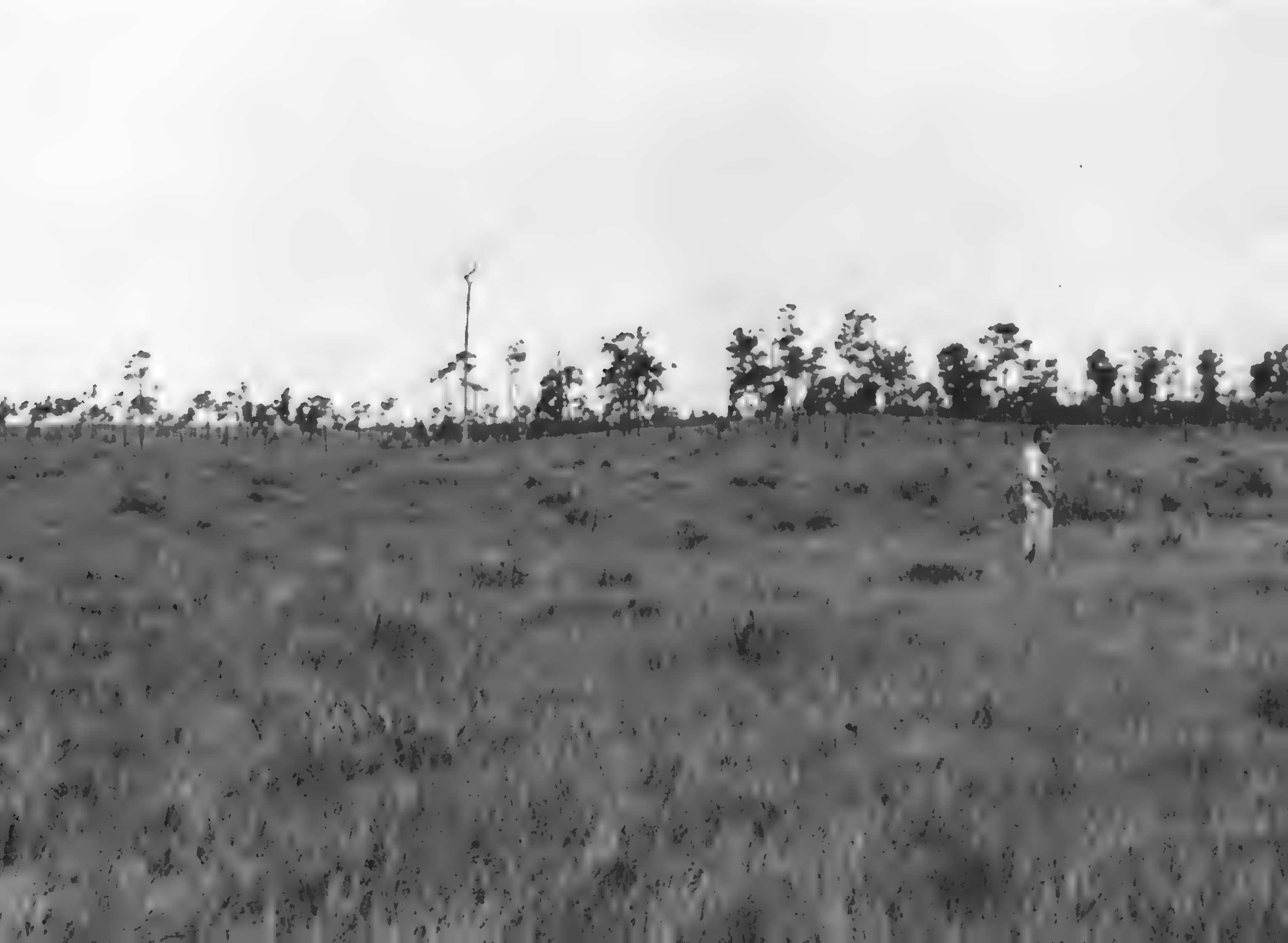


Figure 7 (above). Pine Savanna Area No. 3.

Figure 8 (below). The Grassland Area.



Wide-ranging residents—resident species that use the savanna frequently and importantly, perhaps exclusively in the case of some individuals, but which, as species, also use adjacent, nonsavanna habitats frequently and importantly.

Summer residents—species that differ from permanent residents only by their absence.

Winter residents—species that nest in temperate North America and occur regularly in the savanna during the winter months.

Regular visitors from adjacent broad-leafed forest—resident species that are widespread in broad-leafed forest or forest edge and regularly range into the savanna and may even nest in the pines; all of these species appear to depend on a broad-leafed forest close by for many or most of their activities.

The avifauna of the savanna areas showed little variation in the resident populations from year to year or season to season, except in Area 2, in November 1966, when logging began there. I shall discuss the effects of this on the bird population later. Some of the resident birds were apparently paired the year round, and in August 1965 we noted some, including the Vermilion Flycatcher (*Pyrocephalus rubinus*), Common Bluebird, Hepatic Tanager (*Piranga flava*), and Rusty Sparrow (*Aimophila rufescens*), in family groups. Others, such as parrots and the Common Meadowlark, appeared to maintain pairs within flocks and still others, such as the Black-headed Siskin (*Carduelis notata*) and Chipping Sparrow, formed large flocks in the winter months with no evidence of pairing. The only winter resident recorded within the study areas was the Yellow-throated Warbler (*Dendroica dominica*). I shall discuss the interactions between this species and the resident Grace's Warbler later.

We often saw flocks of mixed species, especially in winter, and we noted the tendency for pairs of different species to concentrate in certain areas even at the height of the breeding season in April, leaving other parts of the savanna virtually devoid of birds. We did not determine whether the attraction of other birds as such was the cause of these concentrations or whether the concentrations simply indicated more favorable ecological conditions, not obvious to us.

We estimated the numbers of breeding territories of the species in each of the study areas (Tables 2 and 3) and used these figures to calculate the bird species diversity for each area. Visitors and migrants, also listed, include other birds recorded in each area, but apparently not within their breeding territories.

Avifauna of the Rain Forest Area

We recorded 116 species within the 10-acre study area. However, we considered less than half of these residents; 14 or 15 were migrants; others we recorded only once. For many species, it is difficult to establish reliable criteria of "residence" in a small section of rain forest. Some are secretive or difficult to see in the crown of tall trees. Others wander in mixed species flocks, following army ant trails or feeding at briefly flowering or fruiting trees. The breeding of different species at different seasons means that some birds are singing on territories while others are silent and inconspicuous.

TABLE 1

Birds of the Pine Savanna in Nicaragua

	Permanent Residents
Accipitridae	*Buteo albicaudatus,* White-tailed Hawk
	B. jamaicensis, Red-tailed Hawk
Falconidae	*Falco sparverius,* American Kestrel
	F. femoralis, Aplomado Falcon
	Polyborus cheriway, Crested Caracara
Phasianidae	*Colinus nigrogularis,* Black-throated Bobwhite
Columbidae	*Columbina minuta,* Plain-breasted Ground Dove
Psittacidae	*Amazona ochrocephala,* Yellow-headed Parrot[1]
Strigidae	*Bubo virginianus,* Great Horned Owl
Trochilidae	*Amazilia cyanocephala,* Red-billed Azurecrown
Picidae	*Dendrocopos scalaris,* Ladder-backed Woodpecker
Tyrannidae	*Pyrocephalus rubinus,* Vermilion Flycatcher
	Muscivora tyrannus, Fork-tailed Flycatcher
Troglodytidae	*Cistothorus platensis,* Sedge Wren
Turdidae	*Sialia sialis,* Common Bluebird
Parulidae	*Dendroica graciae,* Grace's Warbler
Icteridae	*Icterus chrysater,* Yellow-backed Oriole
	Sturnella magna, Common Meadowlark
Thraupidae	*Piranga flava,* Hepatic Tanager
Fringillidae	*Carduelis notata,* Black-headed Siskin
	Loxia curvirostra, Red Crossbill
	Sicalis luteola, Yellow Grass-finch[2]
	Ammodramus savannarum, Grasshopper Sparrow
	Aimophila rufescens, Rusty Sparrow
	A. botterii, Botteri Sparrow
	Spizella passerina, Chipping Sparrow
	Wide-ranging Residents
Cathartidae	*Cathartes aura,* Turkey Vulture
	C. burrovianus, Yellow-headed Turkey Vulture
	Coragyps atratus, Black Vulture
Rallidae	*Laterallus ruber,* Ruddy Crake
	Summer Residents
Caprimulgidae	*Chordeiles minor,* Common Nighthawk
	Caprimulgus maculicaudus, Spot-tailed Nightjar[3]

TABLE 1 *(Continued)*

	Winter Residents
Picidae	*Sphyrapicus varius,* Yellow-bellied Sapsucker
Hirundinidae	*Iridoprocne bicolor,* Tree Swallow[4]
Parulidae	*Dendroica coronata,* Myrtle Warbler *D. dominica,* Yellow-throated Warbler *D. palmarum,* Palm Warbler
	Visitors from Adjacent Broad-leafed Forest
Accipitridae	*Buteo magnirostris,* Roadside Hawk
Falconidae	*Herpetotheres cachinnans,* Laughing Falcon *Falco rufigularis,* Bat Falcon
Columbidae	*Columba cayennensis,* Pale-vented Pigeon *C. speciosa,* Scaled Pigeon
Psittacidae	*Ara macao,* Scarlet Macaw *Amazona autumnalis,* Red-lored Parrot[5] *Aratinga astec,* Olive-throated Parakeet
Strigidae	*Glaucidium brasilianum,* Ferruginous Pygmy Owl
Nyctibiidae	*Nyctibius griseus,* Common Potoo
Caprimulgidae	*Nyctdromus albicollis,* Pauraque
Picidae	*Piculus rubiginosus,* Golden-olive Woodpecker *Dryocopus lineatus,* Lineated Woodpecker *Melanerpes formicivorus,* Acorn Woodpecker[6]
Tyrannidae	*Tyrannus melancholicus,* Tropical Kingbird[7] *Elaenia flavogaster,* Yellow-bellied Elaenia[7]
Hirundinidae	*Progne chalybea,* Gray-breasted Martin
Corvidae	*Psilorhinus morio,* Brown Jay
Parulidae	*Geothylypis poliocephala,* Gray-crowned Yellowthroat

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[1] Apparently feeds only in broad-leafed trees at the edge of the savanna.

[2] Apparently a gregarious species of wandering habits and irregular occurrence.

[3] Not recorded from November to March; presumably absent during that time.

[4] Recorded only in February 1963 when it was abundant.

[5] Found in the savanna as frequently as the Yellow-headed Parrot, but differs in that it uses broad-leafed forest as much as it does the savanna.

[6] Uses the savanna only in the vicinity of oaks (*Quercus oleoides*).

[7] More likely to range out, even territorially, into the savanna from the broad-leafed forest edge than other tyrannids such as *Contopus cinereus, Myiarchus tuberculifer,* and *Myiozetetes similis.*

For calculating the species diversity, I included only those species that we found nesting or on territories in April 1967, or that we recorded more than once in that month and also in March and November 1966 when we made other censuses. This lowers the list to 37 species, a conservative figure, since we doubtless overlooked some inconspicuous forms at one time or another.

We encountered further difficulties in estimating the number of territories. Hummingbird females, for example, may not nest within the territories of conspicuous males; each male in a group of displaying manakins may not secure a mate and nest within the study area; and the study area may represent only a portion of the entire territory of a nesting pair of kites. Such complications, though they may introduce some error into the estimates, are unavoidable. In Table 3, I estimated the number of territories for each of the 37 species believed to be resident in at least part of the study area, and calculated the bird species diversity (BSD) from these figures.

Results

The foliage profiles for all three areas in which we measured the vegetation density agree reasonably well with our impressions of the physiognomy of the total vegetation. The reader may judge this by examining the photographs (Figures 5–10). We may now consider each area from the standpoint of the predicted bird species diversity.

Pine Savanna Area 1

The calculated BSD of 2.08 in this study is close to the figure of 1.98, predicted from the formula derived by MacArthur and MacArthur (1961) on the basis of data gathered in five-acre plots of deciduous woodland in temperate North America. One could interpret this result as a confirmation of the prediction, at least as applied to a habitat that is characteristic of temperate regions despite its location in a tropical latitude and climate. However, the Nicaraguan study area encompasses 25 acres instead of only five, as used by the MacArthurs. Even in the 25 acres, only two of the 10 breeding bird species had more than one pair with territories within the study area. With such low densities of breeding pairs, the size of the study plot definitely affects the diversity figures. For example, if we had censused only five acres within Area 1, we could, assuming that the foliage height density (FHD) was relatively uniform, have obtained a count of three territories and four species (for example, 1, 1, 0.5, 0.5) with a BSD of only 1.23—well below the predicted figure.

The foliage profile and FHD of .731 for five acres of deciduous woodland in Vermont (MacArthur and MacArthur, 1961) appear quite close to the foliage profile and FHD for Pine Savanna Area 1; the Vermont woodland included nine territories of six species; the Nicaraguan Area 1 included 10 territories of nine species. Taken as a whole, the quantitative data suggest that, in terms of bird population density and species diversity, five acres of temperate deciduous woodland is roughly equivalent to 25 acres of tropical pine savanna.

Such comparisons are difficult to evaluate as the pine savanna, in contrast to deciduous woodland, includes only one species of tall tree. Furthermore, pines represent a special type of vegetational resource to which some birds are well-adapted and others not at all. I know of no measurements of FHD in temperate zone pine forests, but there are bird censuses in such habitats from which BSD can be calculated.

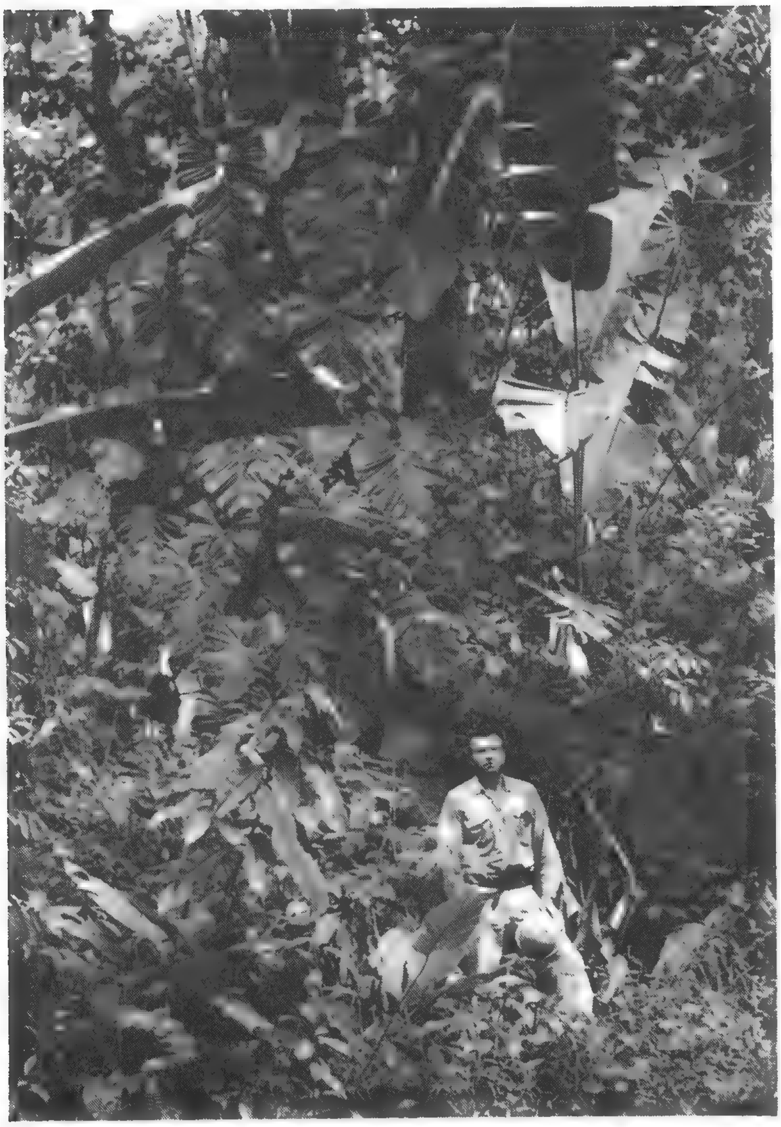

Figure 9. Edge of the Rain Forest Area.

In Georgia, Norris (1951) censused the breeding birds in 43 acres of mature, but recently burned-over, longleaf-pine forest (*Pinus palustris*) with only a light woody undercover and wire-grass (*Aristida*); this habitat appears similar to the Nicaraguan pine savanna. Eliminating one pair of Cardinals (*Cardinalis cardinalis*) and one pair of Yellow-throated Vireos (*Vireo flavifrons*) that depended on patches of broad-leafed vegetation, Norris recorded 15 species and 82.5 breeding pairs (Table 7). Since 25 is about 0.6 of 43, 25 acres should have about 50 pairs and a BSD of 2.13, a figure remarkably close to the BSD of 2.08 for Pine Savanna Area 1, but with five times as many breeding territories.

Assuming (1) that Norris' longleaf-pine area had a FHD similar to that in Savanna Area 1, (2) that the interpolation of figures from 43 to 25 acres is valid, and (3) that the similarities in BSD for the Vermont, Georgia, and Nicaraguan study area are not merely coincidental, it appears that we may expect a BSD of approximately 2.0 in areas of similar foliage profile in (a) temperate deciduous woodland, (b) temperate pine woodland, and (c) tropical pine savanna. But the tropical pine savanna differs in that it is five times as large as the temperate deciduous woodland and includes only one-fifth as many breeding bird territories as the temperate pine woodland. One way or another, the Savanna Area 1 appears to be only one-fifth as "rich" as comparable areas in the temperate zone.

TABLE 2

Species and Numbers of Breeding Territories in the Nicaraguan Pine Savanna

Species	*Area No. 1*	*Area No. 2*	*Area No. 3*
Breeding Species			
Falco sparverius	—	—	0.25
Colinus nigrogularis	—	0.5	0.25
Ara macao (1967) or *Amazona ochrocephala* (1966)	0.5	—	—
Amazilia cyanocephala	1.0	1.0	—
Dendrocopos scalaris	0.5	—	—
Sialia sialis	1.0	—*	—
Dendroica graciae	2.5	2.0	0.5
Geothlypis poliocephala	—	0.5	—
Sturnella magna	1.0	—*	1.0
Piranga flava	1.5	1.5	—
Carduelis notata	1.0	—	—
Aimophila rufescens	1.0	1.0	1.0
Total number of pairs	10.0	6.5	3.0
B.S.D.	2.08	1.67	1.44
Species Recorded, but Apparently Not on Territories			
Coragyps atratus	x	—	—
Herpetotheres cachinnans	x	—	—
Columba speciosa	x	—	—
C. cayennensis	x	x	x
Amazona autumnalis	x	x	x
Bubo virginianus	x	—	—
Chordeiles minor	x	x	x
Piculus rubiginosus	—	x	—
Dryocopus lineatus	—	x	—
Melanerpes formicivorus	x	—	—
Pyrocephalus rubinus	—	—	x
Progne chalybea	x	x	—
Psilorhinus morio	—	x	—
Dendroica dominica	x	x	x
Loxia curvirostra	x	—	—
Aimophila botterii	—	—	x

*Recorded after logging of area; may or may not have bred there.

Figure 10. Rain Forest Area showing varied tree heights.

Davenport (1964, 1965, 1966) repeatedly censused 18.5 acres of Georgia pine forest with 95 per cent *Pinus "caribaea"* (= *P. elliottii*), 4 per cent Sweet Gum (*Liquidamber stryaciflua*), and a patchy undercover of shrubs and seedlings with virtually no grasses. His figures for each of three consecutive years show 22 species and 42 territorial males, 20 species and 41 territorial males, 19 species and 50 territorial males. The number of species in Davenport's Georgia area is higher than in Norris' Georgia area, but some of these such as the Yellow-billed Cuckoo (*Coccyzus americana*) and Hooded Warbler (*Wilsonia citrina*) obviously depend on broad-leafed plants.

Davenport's area seems less like the Nicaraguan pine savanna than does Norris'; but in Davenport's area also there appear to be about 50 breeding territories of pine-dwelling birds in 25 acres. Davenport's three-year average is 44.3 territories in 18.5 acres or about 60 in 25 acres. However, Davenport's list includes about 10 species that are wholly, or largely, dependent on broadleafed vegetation. Very likely, if the larger trees were exclusively pines, these 10 would not occur in the area and there would be close to 50 breeding territories in 25 acres.

One can compare the bird populations of different regions by using the combined weights of all the breeding birds found in equivalent areas of each region. I did this for Savanna Area 1, for the Vermont deciduous woodland of MacArthur, and for the Georgia longleaf-pine forest of Norris. I took the weights of the Nicaraguan savanna birds exclusively from specimens collected there, and obtained the weights for the birds in the Vermont and Georgia areas principally from Hartman (1955) and Norris and Johnston (1958). Though the sample size of each species is sometimes small, the means of the weights are probably adequate for comparison. In practice, it was convenient to average the average weights of males and females of each species and multiply this figure by the number of pairs present. Because pairs were involved, one should double this sum to arrive at the total weight of breeding birds present.

The total weight of the birds for Pine Savanna Area 1 was 468 grams, without the weight of a breeding pair of parrots, which I excluded because they apparently took no food from the savanna and thus were not in the same category as the resident species that fed there exclusively. The weight for the breeding birds in 25 acres of Georgia longleaf-pine forest was 2,680 g, approximately 5.7 times as great. Although these figures are approximations, they conform fairly well to other data that suggest that the tropical pine savanna is only one-fifth as rich in birdlife as a comparable area in the temperate zone.

The weight of the birds from the five-acre deciduous woodland in Vermont is 458 g. This figure, from an area with a vegetational profile similar to that in Savanna Area Number 1, is very close to the figure of 468 g for 25 acres of Area 1 and lends support to the suggestion that, in terms of bird population, 25 acres of tropical pine savanna is ecologically equivalent to five acres of temperate deciduous woodland with a comparable FHD. The three areas had certain taxa in common (Table 8).

I have discussed Savanna Area 1 at length because it appeared to approach the upper limit of numbers of species and individuals that occur in any area of comparable size in the unmixed pine savanna in Nicaragua. Our field parties carefully covered hundreds of acres of this savanna and never encountered a section that appeared to support a greater variety and quantity of birds, even in pure stands of pines that were taller or denser or both.

Pine Savanna Area 2

The presence of a well-developed intermediate layer of pine seedlings and a much denser ground cover results in a FHD of 1.058, and a predicted BSD of 2.59—considerably higher than that for Savanna Area 1. However, the actual BSD, according to our observations was only 1.67, considerably lower than the prediction and lower than the diversity we observed in Area 1.

This is a striking exception to the generalization that the addition of a layer of foliage increases the BSD, but there is a possible ecological explanation. We delimited Area 2 to include only acreage that was unburned for many years, thus supporting a higher growth of ground-cover plants and much denser stands of pine seedlings than in Area 1. This difference eliminated suitable habitat in Area 2 for the Common Bluebird and Common Meadowlark, two species found in Area 1, but did not provide conditions favorable for breeding of other local species.

The pine seedlings are strictly a transient formation in this region. They grow rapidly into tall trees or they are destroyed by fires that are apparently both a cause and a consequence of the savanna environment. A dense growth of herbaceous cover in one corner of Area 2 probably accounted for the inclusion within it of part of a territory of the Gray-crowned Yellowthroat (*Geothlypis poliocephala*), a species not adapted to the exploitation of pine seedlings. Thus, the net effect of the increased density of the vegetation was a reduction in the number of bird species and individuals present.

As the intermediate layer, predominately of pine seedlings, is seldom used by any birds except occasionally by the usually higher ranging Grace's Warbler and Hepatic Tanager, we recalculated the FHD with the assumption that the resident birds recognized only two layers—0 to 3 ft and 3 to 42.26 ft which was the average height of trees higher than 25 ft. This yields an FHD of 0.696 and a predicted BSD of 1.86, a figure considerably closer to our observed BSD of 1.67. It supports the speculation that Area 2 represents essentially a two-layer habitat for birds.

TABLE 3

Birds of the Rain Forest Area

Family	*Species*	*Number of breeding territories*
	Breeding Pairs	
Tinamidae	*Tinamus major,* Great Tinamou	0.5
Accipitridae	*Leptodon cayanensis,* Gray-headed Kite	0.25
Columbidae	*Columba nigrirostris,* Short-billed Pigeon	0.5
Trochilidae	*Phaethornis superciliosus,* Long-tailed Hermit	1.5
	P. longuemareus, Little Hermit	2.0
	Thalurania furcata, Green-crowned Woodnymph	2.0
	Hylocharis eliciae, Blue-throated Goldentail	1.0
	Amazilia candida, White-bellied Emerald	0.25
	Chalybura urochrysia, Bronze-tailed Plumeleteer	1.0
Trogonidae	*Trogon rufus,* Black-throated Trogon	1.0
Picidae	*Centurus pucherani,* Black-cheeked Woodpecker	0.5
	Phloeoceastes guatemalensis, Pale-billed Woodpecker	0.5
Dendrocolaptidae	*Dendrocincla fuliginosa,* Plain-brown Woodcreeper	1.0
Furnariidae	*Sclerurus guatemalensis,* Scaly-throated Leafscraper	0.25
Formicariidae	*Thamnophilus punctatus,* Slaty Antshrike	2.5
	Myrmotherula fulviventris, Fulvous-bellied Antwren	1.0
	M. axillaris, White-flanked Antwren	1.0
	Microrhopias quixensis, Dot-winged Antwren	1.0
	Formicarius analis, Black-faced Antthrush	1.0
	Phaenostictus mcleannani, Ocellated Antthrush	1.0
Pipridae	*Pipra mentalis,* Red-capped Manakin	5.5
Cotingidae	*Laniocera rufescens,* Speckled Mourner	1.0
Tyrannidae	*Megarynchus pitangua,* Boat-billed Flycatcher	1.0
	Terenotriccus erythrurus, Ruddy-tailed Flycatcher	1.0
	Myiobius barbatus, Sulphur-rumped Flycatcher	1.0
	Platyrinchus mystaceus, White-throated Spadebill	0.5
	Pipromorpha oleaginea, Ochre-bellied Flycatcher	3.0
Troglodytidae	*Henicorhina leucosticta,* White-breasted Wood-wren	2.5
Sylviidae	*Polioptila plumbea,* Tropical Gnatcatcher	1.5
Vireolaniidae	*Smaragdolanius pulchellus,* Green Shrike-vireo	1.0
Vireonidae	*Hylophilus decurtatus,* Gray-headed Greenlet	2.5
Parulidae	*Phaeothylypis rivularis,* Buff-rumped Warbler	0.5
Thraupidae	*Euphonia gouldi,* Olive-backed Euphonia	1.0
	Chlorothraupis carmioli, Olive Tanager	2.0
	Habia fuscicauda, Dusky-tailed Ant-tanager	2.5
Fringillidae	*Cyanocompsa cyanoides,* Blue-black Grosbeak	1.0
	Arremon aurantiirostris, Orange-billed Sparrow	0.5
		47.75

TABLE 3 *(Continued)*

Family	*Species*	*Number of breeding territories*
	Visitors and Migrants	
Accipitridae	*Accipiter bicolor,* Bicolored Hawk	
	Buteo magnirostris, Roadside Hawk	
Cracidae	*Penelope purpurascens,* Crested Guan	
Phasianidae	*Odontophorus erythrops,* Rufous-fronted Wood-quail	
	Rhynchortyx cinctus, Tawny-faced Quail	
Columbidae	*Columba cayennensis,* Pale-vented Pigeon	
	C. speciosa, Scaled Pigeon	
	Leptotila cassinii, Gray-chested Dove	
Psittacidae	*Ara macao,* Scarlet Macaw	
	Aratinga astec, Olive-throated Parakeet	
Cuculidae	*Piaya cayana,* Squirrel Cuckoo	
	Neomorphus geoffroyi, Rufous-vented Ground-cuckoo	
Trochilidae	*Threnetes ruckeri,* Band-tailed Barbthroat	
	Florisuga mellivora, White-necked Jacobin	
	Amazilia amabilis, Blue-chested Hummingbird	
	Heliothrix barroti, Purple-crowned Fairy	
Momotidae	*Momotus momota,* Blue-crowned Motmot	
Bucconidae	*Notharchus macrorhynchos,* White-necked Puffbird	
	Malacoptila panamensis, White-whiskered Puffbird	
Ramphastidae	*Pteroglossus torquatus,* Collared Aracari	
	Ramphastos sulfuratus, Keel-billed Toucan	
	R. swainsonii, Chestnut-mandibled Toucan	
Picidae	*Piculus simplex,* Rufous-winged Woodpecker	
	Celeus castaneus, Chestnut-colored Woodpecker	
Dendrocolaptidae	*Dendrocincla anabatina,* Tawny-winged Woodcreeper	
	Glyphorynchus spirurus, Wedge-billed Woodcreeper	
	Xiphorhynchus guttatus, Buff-throated Woodcreeper	
Furnariidae	*Automolus ochrolaemus,* Buff-throated Foliage-gleaner	
	Xenops minutus, Plain Xenops	
Formicariidae	*Cymbilaimus lineatus,* Fasciated Antshrike	
	Myrmotherula schisticolor, Slaty Antwren	
	Myrmeciza exsul, Chestnut-backed Antbird	
	Gymnopithys bicolor, Bicolored Antbird	
	Hylophylax naevioides, Spotted Antbird	
	Grallaria fulviventris, Fulvous-bellied Antpitta	
Pipridae	*Manacus candei,* White-collared Manakin	
	Schiffornis turdinus, Thrush-like Manakin	
Cotingidae	*Carpodectes nitidus,* Snowy Cotinga	
	Rhytipterna holerythra, Rufous Mourner	
Tyrannidae	*Contopus* sp., Pewee	
	Onychorhynchus mexicanus, Northern Royal-flycatcher	
	Platyrinchus coronatus, Golden-crowned Spadebill	
	Rhynchocyclus brevirostris, Eye-ringed Flatbill	
	Todirostrum cinereum, Common Tody-flycatcher	
	Oncostoma cinereigulare, Northern Bentbill	
	Ornithion semiflavum, Yellow-bellied Tyrannulet	

TABLE 3 *(Continued)*

Family	*Species*	*Number of breeding territories*
Corvidae	*Psilorhinus morio,* Brown Jay	
Troglodytidae	*Thryothorus castaneus,* Bay Wren	
	Cyphorhinus phaeocephalus, Song Wren	
Mimidae	*Dumetella carolinensis,* Common Catbird	
Turdidae	*Hylocichla mustelina,* Wood Thrush	
Sylviidae	*Ramphocaenus melanurus,* Long-billed Gnatwren	
Vireonidae	*Vireo olivaceus,* Red-eyed Vireo	
	Hylophilus ochraceiceps, Tawny-crowned Greenlet	
Coerebidae	*Chlorophanes spiza,* Green Honeycreeper	
	Cyanerpes lucidus, Shining Honeycreeper	
	Dacnis cayana, Blue Dacnis	
Parulidae	*Mniotilta varia,* Black-and-white Warbler	
	Dendroica magnolia, Magnolia Warbler	
	D. pensylvanica, Chestnut-sided Warbler	
	D. castanea, Bay-breasted Warbler	
	Seiurus aurocapillus, Ovenbird	
	S. noveboracensis, Northern Waterthrush	
	S. motacilla, Louisiana Waterthrush	
	Oporornis formosus, Kentucky Warbler	
	Wilsonia canadensis, Canada Warbler	
Icteridae	*Zarhynchus wagleri,* Chestnut-headed Oropendola	
	Gymnostinops montezuma, Montezuma Oropendola	
	Cacicus uropygialis, Scarlet-rumped Cacique	
	Icterus galbula, Baltimore Oriole	
Thraupidae	*Euphonia lauta,* Yellow-throated Euphonia	
	Tangara larvata, Golden-masked Tanager	
	Ramphocelus passerinii, Scarlet-rumped Tanager	
	Piranga rubra, Summer Tanager	
	Lanio leucothorax, White-throated Shrike-tanager	
	Tachyphonus luctuosus, White-shouldered Tanager	
Fringillidae	*Saltator maximus,* Buff-throated Saltator	
	Caryothraustes poliogaster, Black-faced Grosbeak	
	Oryzoborus funereus, Thick-billed Seed-finch	

The bird fauna in Area 2 changed as conditions in and around it changed. As previously mentioned, 10 acres of small pine seedlings and grass, adjacent to the 15-acre study plot, were burned about four months before the first census in August 1965, and at that time were devoid of birds. By March 1966, the ground-cover plants in the burned area showed considerable regrowth and we recorded the Common Meadowlark and Common Bluebird as visitors.

Unfortunately, logging operations that coincided with my next visit, in November 1966, removed most of the larger straight pines, knocked down some seedlings, and scattered many sawed-off branches and tree tops. On 28 November, I saw a Golden-olive Woodpecker (*Piculus rubiginosus*) and a Lineated Woodpecker (*Dryocopus lineatus*) foraging in some of the remaining larger pines, especially those damaged by the logging. I had not recorded them previously and never saw them again in that area. In addition, we saw a Gray-crowned Yellowthroat foraging among fallen pine branches in the center of the area, well away from the corner where this species previously stayed. By 22 April 1967, 20 months after our first census, the bird fauna of Area 2 showed a loss of one pair each of the Red-billed Azurecrown (*Amazilia cyanocephala*), Grace's Warbler, and Hepatic Tanager, and the addition of one pair of Rusty Sparrows and part of the territory of a pair of Common Meadowlarks; we again noted the Gray-crowned Yellowthroat in the center of the area.

Pine Savanna Area 3

Despite the permanent stream running through it, Area 3 was extremely poor both in numbers of species and numbers of individuals. The 25 acres apparently supported as breeding residents only five species at most and included the entire territories of only two of these. The BSD equaled 1.44, less than either Areas 1 or 2. The low BSD predicts a FHD of about 0.5, which seems reasonable in comparison with Area 1. Except along the stream, the density of the vegetation, both trees and ground cover, was perhaps near the lower limit required by most savanna birds. Thus, the pines were too widely spaced for the Grace's Warbler and Hepatic Tanager; the shrubs, grasses, and sedges were too low and too sparse for most ground-dwelling forms. The openness possibly attracted the American Kestrel (*Falco sparverius*) and Vermilion Flycatcher, but may not have provided enough food for their support.

Grassland Area

This five-acre area apparently did not include even part of the territories of any breeding birds. We saw the Common Meadowlark and Rusty Sparrow in the vicinity but not within the boundaries of the study area. Only six or seven of the species listed in Table 1 are potential nesters in grassland, and most of these are either sparsely and locally distributed or found only near stream-bordered thickets or wet areas. We walked across many acres of pure grasslands outside the study plot and invariably found birds scarce or absent. I attribute this to the paucity of grassland-adapted species in the isolated habitat and to the apparent scarcity of food for such species.

Rain Forest Area

The FHD, calculated from density measurements at the same three levels as in the pine savanna, is 0.3813. This low figure results from the great difference in the density of the different layers; the one above 20 ft, which averages 54.3 ft high, is very dense compared to the others. Nevertheless, the foliage profile fits my impression of the forest reasonably well.

The predicted BSD with this FHD is only 1.23, but we recorded a BSD of 3.64. MacArthur *et al.* (1966) also recorded high BSD's—3.393 and 3.378—in similar rain-forest habitats in Panama, and their figures are much higher than predicted from a FHD calculated from measurements at three levels (0–2, 2–25, >25). MacArthur and his associates suggested that birds may distinguish four layers of vegetation (0–2, 2–10, 10–50, >50). A calculation of FHD on the basis of four layers fits better the regression line derived from three-layer measurements in the temperate zone. In support of the four-layer division, they cited Slud (1960), who proposed recognition of five levels of the forest habitat at Finca "La Selva," Costa Rica.

In the Nicaraguan Rain Forest Area, my impression was that the 10 to 50 ft layer did not correspond either to a pattern of foliage density or to a distinct stratum recognized and used by certain species of birds. Because Slud's Costa Rican area included all species of birds that we recorded in the Nicaraguan rain forest plot, and because he based his designation of levels on observations made during a year's continuous residency, I attempted to convert his five semiqualitative divisions into units which, when applied to my study area, permitted a calculation of FHD at five levels.

The resulting conversion (Table 4) gives Slud's terminology and my estimates of the vertical extent of each division. With the five layers, the FHD becomes 1.03+ and the predicted BSD equals 2.54, closer to the observed BSD of 3.64 than when calculated at three levels, but nevertheless low. Actually, only the subdivision of the dense foliage above 20 ft into two layers has much effect on the FHD figure. If we use only four layers (0–3, 3–20, 20–50, 50–74.3) the FHD equals 1.00 and the BSD equals 2.47. However, my field observations do not support the supposition that birds distinguish two layers in the upper levels of the forest. Most bird species found at those levels appeared to range freely from about 20 ft above the ground to the tops of the trees. A comparison of my Nicaraguan census data (Table 4) with Slud's species lists for the middle forest and canopy shows that, in Nicaragua, all canopy species except the Gray-headed Kite (*Leptodon cayanensis*) and the Green Shrike-Vireo (*Smaragdolanius pulchellus*) also range through the middle forest level, and all 16 middle forest species also occur either in the canopy or in the high understory level.

We cannot exclude the possibility of subtle partitioning by the birds, but calculations based on further divisions of this type of habitat are bound to raise the figure for FHD and hence the predicted BSD. A better fit of high BSD figures to predicted values is thus inevitable and not necessarily confirmatory. Orians (1969) also doubted that finer division by birds of the layers of the tropical forest is the primary factor responsible for the relatively large number of bird species present, but he now informs me (1971, pers. commun.) that he has new evidence that such partitioning is importantly involved.

The Rain Forest Area of only 10 acres had 37 species on territories and 79 additional species as visitors. These data raise questions about the use of census figures. If an area has more than twice as many visiting species as species on territories, should we omit the "visitors" from calculations of species diversity? These "visitors" use food and other resources of the area, often with apparent regularity; they must affect the approximately equally common "residents" and have an ecological impact on the habitat. Yet measurements of species diversity, based on the number of species with breeding territories in a given area, exclude them. Even ignoring the visitors, the large number of resident breeding species results in a high diversity figure for the rain forest.

Orians (1969) dealt with similar censusing problems in Costa Rica by basing his BSD calculations on "... the total number of species encountered on each of the sites and not upon some measure requiring an estimate of their proportional representation." I share Orians' despair in attempting to get accurate data on the number of territories of rain-forest species in a given area. However, I feel justified in making estimates as my study area was 10 acres—large enough to include fully the territories of many species—and as several observers made many censuses at different seasons over two years.

It is difficult to compare my results with Orians'; he used a different method of measuring the vegetation profile (MacArthur and Horn, 1969) and calculated BSD without estimating proportional representation. His data for a three-acre plot at La Selva, a habitat probably similar to my study area, included FHD (four layers) of .40 and BSD of 1.65. My figures for Nicaragua are quite different on both counts. I have discussed them with Orians and we cannot tell whether our different methods or other factors are primarily responsible.

Discussion

Using the data above and additional information from observations within and near the study areas, I now consider the questions posed in the introduction.

Question 1

What are the precise qualitative and quantitative differences between the avifaunas of measured areas of tropical pine savanna and of adjacent broad-leafed forest?

I have outlined and discussed in part the avifaunal differences between the different study areas and habitat types. I found no species breeding in both the savanna and rain forest study areas, and recorded only three species—Pale-vented Pigeon (*Columba cayennensis*), Scaled Pigeon (*C. speciosa*), Brown Jay (*Psilorhinus morio*)—as visitors in both. The Scarlet Macaw (*Ara macao*) proved to be a special case. Although it feeds only in broad-leafed forest and we recorded it as a visitor in the Rain Forest Area, one pair nested in Pine Savanna Area 1 in April 1967. Otherwise, despite the proximity of the savanna and rain forest areas and the similarity in many of the large-scale environmental features such as day length, climate, elevation, etc., their avifaunas are almost totally different, both in the numbers of different species and numbers of individuals.

Question 2

Within the tropical savanna, what are the differences between the bird populations in pines with little understory or seedling, pines with more understory and abundant pine seedlings of various heights, and the treeless savanna with grasses, sedges, and a few shrubs?

The pine savanna with little shrubby or herbaceous understory and few seedlings supports a more diverse and abundant avifauna than an area where such growth is prevalent. However, if the pines are too far apart and the ground cover too sparse, the avifauna is also sparse. The treeless grass savanna is particularly impoverished.

Question 3

Are the differences in bird populations in the various habitats predictable on the basis of their foliage profiles as proposed by MacArthur and MacArthur (1961)?

The differences are not predictable purely on the basis of different foliage profiles, but they are accountable on other ecological grounds.

Question 4

How do the bird populations of the tropical habitats compare, in numbers of species and numbers of individuals, with bird populations in temperate-zone habitats?

TABLE 4

Birds of the Rain Forest

Occurrence in one or more of Five Vertical Layers of Vegetation

Residents	_Visitors_	_Migrants_
	Forest Floor (0–3 feet)	
Tinamus major	_Odontophorus erythrops_	_Seiurus aurocapillus_
Sclerurus guatemalensis	_Rhynchortyx cinctus_	_S. noveboracensis_
Formicarius analis	_Leptotila cassinii_	_S. motacilla_
Phaenostictus mcleannani	_Neomorphus geoffroyi_	
_Henicorhina leucosticta_*	_Mymeciza exsul_	
Phaeothlypis rivularis	_Gymnopithys bicolor_	
Arremon aurantiirostris	_Grallaria fulviventris_	
	_Cyphorhinus phaeocephalus_*	
	Low Understory (3–6 feet)	
_Phaethornis superciliosus_*	_Threnetes ruckeri_*	_Dumetella carolinensis_
_P. longuemareus_*	_Automolus ochrolaemus_*	_Hylocichla mustelina_*
_Thamnophilus punctatus_*	_Hylophylax naevioides_	_Dendroica magnolia_*
Platyrinchus mystaceus	_Manacus candei_	_Oporornis formosus_
_Henicorhina leucosticta_*	_Schiffornis turdinus_	
_Habia fuscicauda_*	_Thryothorus castaneus_	
_Cyanocompsa cyanoides_*	_Cyphorhinus phaeocephalus_*	
	_Ramphocaenus melanurus_*	
	High Understory (6–20 feet)	
_Phaethornis superciliosus_*	_Accipiter bicolor_	_Hylocichla mustelina_*
_P. longuemareus_*	_Threnetes ruckeri_*	_Mniotilta varia_
Thalurania furcata	_Florisuga mellivora_	_Dendroica magnolia_*
Hylocharis eliciae	_Amazilia amabilis_	_D. castanea_*
Amazilia candida	_Momotus momota_	_Wilsonia canadensis_
Chalybura urochrysia	_Notharchus macrorhynchos_	
_Trogon rufus_*	_Malacoptila panamensis_	
_Phloeoceastes guatemalensis_*	_Celeus castaneus_*	
_Dendrocincla fuliginosa_*	_Dendrocincla anabatina_	
_Thamnophilus punctatus_*	_Glyphorynchus spirurus_*	
Myrmotherula fulviventris	_Xiphorhynchus guttatus_*	
_M. axillaris_*	_Automolus ochrolaemus_	
_Microrhopias quixensis_*	_Xenops minutus_*	
_Pipra mentalis_*	_Cymbilaimus lineatus_	
_Laniocera rufescens_*	_Myrmotherula schisticolor_	
_Megarynchus pitangua_*	_Onychorhynchus mexicanus_	
_Terenotriccus erythrurus_*	_Platyrinchus coronatus_	
_Myiobius barbatus_*	_Rhynchocyclus brevirostris_*	
_Pipromorpha oleaginea_*	_Todirostrum cinereum_	
_Polioptila plumbea_*	_Oncostoma cinereigulare_	
_Euphonia gouldi_*	_Ornithion semiflavum_	
Chlorothraupis carmioli	_Psilorhinus morio_*	
_Habia fuscicauda_*	_Ramphocaenus melanurus_*	

TABLE 4 _(Continued)_

Residents	_Visitors_	_Migrants_
_Cyanocompsa cyanoides_*	_Hylophilus ochraceiceps_	
	Euphonia lauta	
	Ramphocoelus passerinii	
	_Lanio leucothorax_*	
	Saltator maximus	
	Oryzoborus funereus	
	Middle Forest (20–50 feet)	
_Columba nigrirostris_*	_Buteo magnirostris_	_Contopus_ sp.
_Trogon rufus_*	_Aratinga astec_*	_Vireo olivaceus_
_Centurus pucherani_*	_Pteroglossus torquatus_*	_Dendroica magnolia_*
_Phloeoceastes guatemalensis_*	_Ramphastos sulfuratus_*	_D. pensylvanica_
_Dendrocincla fuliginosa_*	_R. swainsonii_*	_D. castanea_*
_Myrmotherula axillaris_*	_Piculus simplex_	_Icterus galbula_
_Microrhopias quixensis_*	_Celeus castaneus_*	_Piranga rubra_
_Pipra mentalis_*	_Xenops minutus_*	
_Laniocera rufescens_*	_Glyphorynchus spirurus_*	
_Megarynchus pitangua_*	_Xiphorhynchus guttatus_*	
_Terenotriccus erythrurus_*	_Rhynchocyclus brevirostris_*	
_Myiobius barbatus_*	_Ornithion semiflavum_*	
_Pipromorpha oleaginea_*	_Psilorhinus morio_*	
_Polioptila plumbea_*	_Chlorophanes spiza_*	
_Hylophilus decurtatus_*	_Gymnostinops montezuma_*	
_Euphonia gouldi_*	_Cacicus uropygialis_*	
	_Tangara larvata_*	
	_Lanio leucothorax_*	
	_Tachyphonus luctuosus_*	
	_Caryothraustes poliogaster_*	
	Canopy (above 50 feet)	
Leptodon cayanensis	_Penelope purpurascens_	
_Columba nigrirostris_*	_Columba cayennensis_	
_Centurus pucherani_*	_C. speciosa_	
_Phloeoceastes guatemalensis_*	_Ara macao_	
_Megarynchus pitangua_*	_Aratinga astec_*	
_Myiobius barbatus_*	_Piaya cayana_	
_Pipromorpha oleaginea_*	_Heliothryx barroti_	
_Polioptila plumbea_*	_Pteroglossus torquatus_*	
Smaragdolanius pulchellus	_Ramphastos sulfuratus_*	
_Hylophilus decurtatus_*	_R. swainsonii_*	
_Euphonia gouldi_*	_Carpodectes nitidus_	
	Rhytipterna holerythra	
	_Rhynchocyclus brevirostris_*	
	_Chlorophanes spiza_*	
	Cyanerpes lucidus	
	Dacnis cayana	
	Zarhynchus wagleri	
	_Gymnostinops montezuma_*	
	_Cacicus uropygialis_*	
	_Tangara larvata_*	
	_Lanio leucothorax_*	
	_Tachyphonus luctuosus_*	
	_Caryothraustes poliogaster_*	

*Occurs in more than one layer.

The bird populations of the richest area of tropical pine savanna are equivalent to about one-fifth of the populations in a temperate-zone area of the same size and similar habitat. The populations of 25 acres of tropical pine savanna are also approximately equivalent to the populations in five acres of temperate-zone deciduous woodland with a similar foliage profile.

Question 5

Does competition restrict any species in its use of either habitat?

Competition must influence restriction to habitat to some extent; otherwise one must assume that no species from either the pine savanna or the rain forest would eventually colonize the other habitat even if it lacked an avifauna of its own. Evidence that suggests competitive exclusion or restriction would include (1) direct conflict between potential competitors, (2) incomplete colonization of one habitat by species characteristic of another, or (3) replacement of species characteristic of one habitat by morphologically and behaviorally similar forms in the other.

I never observed any direct conflicts that suggest competition between pine-savanna and rain-forest bird species. The only frequent interspecific conflicts were between Grace's Warblers and Yellow-throated Warblers in the pines. I shall discuss this more fully under Question 8.

Pine Savanna.—Most permanent resident species characteristic of the pine savanna showed no tendency to invade or colonize the rain forest. This is not surprising as most of these species have feeding habits that require open habitat, and some of them appear to be specifically adapted to pine trees. The Red Crossbill obviously depends on pine seeds; the Chipping Sparrow seems to show a distinct preference for pine foliage (Klopfer, 1963); and the Grace's Warbler is almost completely restricted to pines (Webster, 1961), although there is no obvious reason why, with its bark-searching, foliage-gleaning, and flycatching methods of feeding, it could not gather food successfully in the broad-leafed trees at the forest edge. No other resident species forages in the edge situations the way the Grace's Warbler forages in the pines; yet I have never seen this warbler alight, even momentarily, in any tree except a pine.

The Hepatic Tanager is only slightly less restricted to the pines; occasionally, it goes to other trees or shrubs at the edge of the rain forest. The northern populations of this tanager—western United States to northern Nicaragua—all seem to be pine-forest or pine-oak-forest dwellers; the Nicaraguan lowlands constitute a gap in the range (Howell, 1965), and the southern populations—from Costa Rica into South America—have a wide distribution in non-coniferous forests. The most probable potential competitors of this tanager that occur in the broad-leafed forest in Nicaragua also occur farther south; therefore, it appears unlikely that competition restricts these tanagers to the pine savanna.

Only three pine-savanna species appear to be potential colonizers of the broad-leafed forest in that some individuals regularly visit the broad-leafed forest edge. The Yellow-headed Parrot (*Amazona ochrocephala*) apparently feeds only along this edge; the Red-billed Azurecrown frequently feeds at flowering plants along the borders of watercourses and other wet places; the Yellow-backed Oriole (*Icterus chrysater*) most often occurs near the interface of the pines and broad-leafed forest. We saw none of these species deeper in the rain forest, even in the clearings. I shall discuss possible competitive interactions between these and other species below.

The rain-forest and forest-edge species most likely to attempt complete colonization of the savanna are those recorded in Table 1 as regular visitors, and we may group them according to feeding habits: Raptors, three falconiforms and one owl; non-pine feeders, three parrots and two pigeons; bark and tree-trunk feeders, three woodpeckers; aerial insect-feeders, two caprimuligiforms, two tyrannids, and one swallow; insect gleaners, Gray-crowned Yellowthroat; opportunistic omnivore, Brown Jay.

The visiting raptors differ in size and habits from their closest pine-savanna counterparts, but competition with the residents for the limited food resources of the savanna may prevent the visitors from becoming residents. The scarcity of nest holes of suitable size may also be a limiting factor for two of the falcons and the owl.

The visiting species that do not feed in pines depend on habitats other than the savanna for food, although the Pale-vented Pigeon sometimes feeds on mistletoe berries in the pines. The visiting parrots do not appear to require an open habitat, and none, including the resident Yellow-headed Parrot, feeds on pine seeds, a habit that makes *Rhynchopsitta* of Mexico a true pine-forest bird. Probably the only important competition between visiting non-pine feeders and pine-savanna residents is for nesting holes.

It is difficult to believe that competition from the scarce, small resident Ladder-backed Woodpecker (*Dendrocopos scalaris*) prevents full occupancy of the pine savanna by the three larger species of visiting woodpeckers. The Acorn Woodpecker (*Melanerpes formicivorus*) does not venture far from the vicinity of large oaks, and the savanna may not provide adequate resources for resident populations of the other two woodpeckers. The scarcity in the pines of species that excavate large holes may limit the invasions of other hole-nesting species, as mentioned above.

Competition may influence the population size and distribution within the savanna habitat of the aerial insect-catchers, but in this feeding category the savanna has more visitors than residents. I believe that the visitors are restricted because they are unable to sustain themselves in the savanna habitat, with or without competition from residents, except when close to the broad-leafed forest.

The Gray-crowned Yellowthroat is adapted primarily to gleaning insects from herbaceous plants near the ground. Although some of the resident fringillids doubtless obtain some insects from this vegetational stratum, there is no similar adaptive type among the pine-savanna residents. I believe it is not competition that limits this species but a lack of its microhabitat—the herbaceous growth that occurs in the pine savanna only near wet areas.

In the savanna, no resident species resembles the Brown Jay in morphology and behavior. The pines offer little food and the other woody plants are too sparse to provide adequate sustenance for this large jay which forages primarily in trees and shrubs. Brown Jays cannot readily obtain food in the dense savanna grasses and sedges, and open ground is usually quite barren. Hence the species would probably not colonize the pine savanna fully, even in the absence of resident birds.

As competition may be important between superficially dissimilar species and not important between apparently similar ones, it is difficult to say with assurance which forms are truly "replacing" one another in the different habitats. Congeneric status is often a useful criterion as it often indicates a similarity of adaptive characters. Five genera—*Buteo, Falco, Amazona, Amazilia,* and *Icterus*—are represented by different species in both types of habitat. I have discussed above the possible competitive interactions between the species of the first three genera. In addition to those species listed in Tables 1 and 3, we frequently recorded the Cinnamon Hummingbird (*Amazilia rutila*), Rufous-tailed Hummingbird (*A. tzacatl*), and the Black-cowled Oriole (*Icterus prosthemelas*) in broad-leafed forest or forest edge near the study areas.

It is not unlikely that the Cinnamon Hummingbird which, like several savanna residents, inhabits arid semi-open regions in most of its range would colonize the pine savanna if the Red-billed Azurecrown were absent. The Rufous-tailed Hummingbird, White-bellied Emerald (*Amazilia candida*), and Blue-chested Hummingbird (*A. amabilis*) are probably not potential colonizers of the pines, but competition from them and the Cinnamon Hummingbird may limit penetration by the Red-billed Azurecrown into the broad-leafed thickets and rain-forest edges.

In the savanna region the Yellow-backed Oriole inhabits primarily the pines, but in the highlands of Nicaragua, it inhabits varied vegetational associations including pines and broad-leafed forest. In the savanna, I observed this species probing in the crevices of pine bark and foraging in the mistletoe and bromeliads in the pines; it also used the oaks, palms, and other broad-leafed trees along creeks and thickets. Although the much smaller Black-cowled Oriole is fairly common along the edge of the rain forest, I never saw the two species together.

If competition is influential in maintaining ecological separation of these two species, I suspect that it limits the local distribution of the Yellow-backed rather than that of the Black-cowled. We did not record the Yellow-tailed Oriole (*Icterus mesomelas*), which is more like the Yellow-backed in size and color than is the Black-cowled, in northeastern Nicaragua. A few Baltimore Orioles (*I. galbula*) visit the pine savanna occasionally in migration and in winter but I saw no indication that this species influences the activities of the Yellow-backed Oriole.

In summary, I believe that the particular adaptations and requirements of each species play a more important role than does interspecific competition in preventing the successful cross-colonization of these adjacent, but very different, habitats. I doubt that many pine-adapted species would colonize the rain forest even if it lacked a resident avifauna, and I also doubt that many rain-forest species could successfully invade the savanna where the sparse vegetation limits both food and cover. Nevertheless, the pine savanna, unlike the rain forest, gives the impression of an unsaturated habitat, one that could accommodate other adaptive types as well as denser populations of some resident species. I shall consider these points in a following section.

Rain Forest.—The rain-forest habitat, with its large and diverse avifauna (Table 3), requires a somewhat different analysis. Table 4 shows that, with rare exceptions, every resident species within a given forest level differs clearly from every other species in that level in one or more characteristics relevant to competition—in body size, bill size and/or shape, method of feeding, type of food taken, or the usual microhabitat it occupies.

Among the residents, we recorded only two pairs of congeneric species (species in the same genus)—two hummingbirds, the Long-tailed Hermit (*Phaethornis superciliosus*) and the Little Hermit (*P. longuemareus*), and the Fulvous-bellied Antwren (*Myrmotherula fulviventris*) and the White-flanked Antwren (*M. axillaris*). The two hummingbirds differ greatly in size. The two antwrens are generally similar except for color pattern, but the White-flanked is somewhat smaller, has a more slender bill, and seems to move about more quickly.

The birds of the ecologically complex rain forest appear to reduce or avoid interspecific competition by the same means that we observed in the simpler pine savanna—that is, each resident species differs from the others by distinct morphological and behavioral characters that diminish overlap in foraging and other activities. However, even considerable differences in morphology and in general foraging do not necessarily mean little or no competition. Willis (1966a) and Morse (1967) showed, by field studies, that the feeding activities of greatly different species—the Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) and the Ocellated Antthrush (*Phaenostictus macleannani*), the Brown-headed Nuthatch (*Sitta pusilla*) and the Pine Warbler (*Dendroica pinus*)—are competitive and that the competition may strongly influence foraging behavior. Since these competing species are morphologically dissimilar and belong to different families, one could not have predicted the competition by examining museum skins, by calculations from measurements in Ridgway's "Birds of North and Middle America," or even by observing them casually in the field. Examples such as these impose a measure of caution regarding any conclusions about interspecific competition—or lack of it—between dissimilar species.

The number of species, 37, with at least part of the breeding territory within the 10 acres of rain forest is much greater than the corresponding number in the 25 acres of pine savanna. The figure for the rain forest is also greater than for any area of comparable size in a variety of temperate-zone habitats in North America, as reported in *Audubon Field Notes* (1966). In data from 86 different censuses, all areas containing more than 30 territorial species were larger, usually much larger, than 10 acres. However, the number of temperate-zone males per species were proportionately greater in the temperate-zone plots than in the rain forest, and the number of visiting species was proportionately less. These data provide one more example of the well-known phenomenon of tropical diversity—more species but fewer individuals of each species than in the temperate zone—for which many population ecologists and other biologists have proposed particular, or general, explanations.

Klopfer and MacArthur (1960; 1961), who dealt specifically with Neotropical birds, proposed that (1) the environmental stability of the tropics favors more stereotyped behavior patterns, which results in smaller, more restricted niches, and (2) this stability in availability of resources permits greater niche overlap, which furthers—or allows—the coexistence of many very similar species and thus increases diversity. They assumed that non-passerines are more stereotyped in behavior than passerines and claimed that the proportion of individuals of non-passerines to passerines increases with decreasing latitude, thus supporting their hypothesis. They also noted that some tropical congeneric species that may feed together differ only slightly in bill length and presumably use many of the same food resources—an example of niche overlap. Winterbottom (1964), Simpson (1964), and Schoener (1965) discussed these suggestions critically, and I shall consider them later in relation to the pine-savanna populations.

It is difficult to compare the proportion of non-passerines to passerines in the Nicaraguan rain forest with the Klopfer and MacArthur data because their figures are for territorial males per species per 100 acres. Considering the patchy and local distribution of many rain-forest species, I believe that extrapolating the census data from my 10-acre study area by multiplying by 10 would be highly misleading and that the censusing of an additional 90 acres of similar habitat would undoubtedly add many species, both non-passerine and passerine, in irregular abundance.

Considering only the data for 10 acres, one finds a high proportion of non-passerines to passerines—about 24 per cent of the resident males were non-passerines. However, more than half of these were hummingbirds, and if we exclude them, the proportion of non-passerines to passerines is less than 10 per cent. These data clearly do not test the validity of the Klopfer and MacArthur proposal dealing with the non-passerine to passerine ratio. Furthermore, only two pairs of congeneric species resided in the study area and one cannot safely account for the high degree of diversity on the basis of coexistence of groups of similar species with overlapping requirements that finely partition the available resources.

MacArthur *et al.* (1966) censused seven different plots in Panama including both young and mature forest. Out of a combined total of over 90 species, only three pairs of congeneric species held territories in a subplot large enough to include 25 pairs of birds. In all three pairs—Keel-billed Toucan (*Ramphastos sulfuratus*) and Chestnut-mandibled Toucan (*R. swainsonii*), Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) and Black-striped Woodcreeper (*X. lachrymosus*), and Yellow-billed Elaenia (*Elaenia flavogaster*) and Lesser Elaenia (*E. chiriquensis*)—the species differ considerably in size.

Skutch (1966) carefully censused the breeding birds of a 3.75-acre area in Costa Rica for each of three successive years. Of the three-year total of 38 species, he found only the following congeneric forms: Blue-chested Hummingbird and Rufous-tailed Hummingbird, one nest of each in one year; Social Flycatcher (*Myiozetetes similis*) and Gray-capped Flycatcher (*M. granadensis*), both with several nests in two out of three years; and Golden-masked Tanager (*Tangara larvata*), Silver-throated Tanager (*T. icterocephala*), Bay-headed Tanager (*T. gyrola*), and Speckled Tanager (*T. chrysophrys*), two or three of the four species nesting each year. Skutch censused a partly cleared, relatively predator-free area that included planted fruit trees and a feeding tray continuously supplied with bananas. His censuses, like those of MacArthur *et al.* (1966), indicate that, in a specific small area, the high diversity of species is not caused by great numbers of similar congeneric forms.

Visitors.—The large number of visitors recorded in the Nicaraguan study (Table 3) includes a number of congeners of the resident species as well as other similar forms. From a list based on specimens collected in such an area, one could draw the seemingly reasonable but erroneous conclusion that the area supported a large number of very similar species as coexisting nesting birds.

In a specific area at any given time of year, the visitors may be (1) nonbreeding birds—either immatures or adults that have nested or will nest; or (2) breeding birds with territories in another area but with a wide cruising range, or which join mixed species flocks that may wander widely, following army ant trails or feeding in trees and shrubs that flower and fruit profusely but briefly. (See Willis, 1965b, regarding superabundance of insect food exposed by army ants.)

My term "breeding resident" may be somewhat imprecise and ambiguous, for the residents of one area may be visitors in another. However, similar and potentially closely-competing species, although living in the same geographical area, may have their breeding territories so spaced out and scattered that there is little spatial overlap between them except when these species exploit superabundant food. Whether such spacing results from active competition and aggression between species or from slight differences in habitat preference may vary with the species in question. Given the great complexity of the vegetation and the patchy distribution of microhabitats in a tropical rain forest, one would expect that—in a group of similar species—some would have an advantage over others only in certain microhabits; other species would be less specialized; and one or a few quite versatile. This means that some species would be rare and local, others more abundant in varying degrees, and perhaps one or a few almost ubiquitous. Such distributional patterns are particularly frequent in the tropics.

Question 6

Considering the composition of the bird species in both habitats, what may we infer about competition, niche size and overlap, and the partitioning of resources between species and between individuals within a species?

As the number of permanent and summer-resident bird species in the savanna is small, we may consider the entire avifauna instead of only those species recorded in the study areas.

Even rather small differences in body size, in food-getting appendages, or in behavior may reduce or eliminate overlap among birds in the use of critical resources within a shared environment. (See Grant, 1968, for a recent review.) Given such differences "... there can be as many species as there are proportions of the resources that can be counted on from season to season" (MacArthur and Levins, 1964).

Table 5 groups the breeding birds of the pine savanna according to their principal food habits; I have omitted the wide-ranging cathartid vultures and the erratic Yellow Grass-finch (*Sicalis luteola*). With the exception of the buteos and some of the fringillids, every species in each group is clearly distinct from every other on the basis of the kind, size, or location of the food it takes or the manner in which it obtains the food. With this virtual absence of feeding overlap among the resident birds, the pine savanna provides a model of a habitat with a minimal—perhaps subminimal—number of species representing different adaptive types.

Of the 27 forms listed, there are only three pairs of congeneric species: White-tailed Hawk (*Buteo albicaudatus*) and Red-tailed Hawk (*B. jamaicensis*); Aplomado Falcon (*Falco femoralis*) and American Kestrel; Rusty Sparrow and Botteri's Sparrow (*Aimophila botterii*). The two buteos are similar in size and foraging habits; the White-tailed Hawk is much more abundant than the Red-tailed Hawk. Stevenson and Meitzen (1946) characterized the White-tailed Hawk in Texas as an opportunistic feeder that frequently foraged at the edges of prairie fires; it fed on insects and all classes of small vertebrates, frequently including meadowlarks and Common Bobwhites (*Colinus virginianus*). Obviously the Nicaraguan savanna provides the kind of foraging conditions and food resources that the White-tailed exploits successfully. The Red-tailed Hawk feeds primarily on rodents, at least in open habitats, but rodents and other mammals are scarce in the savanna. The evidence suggests that the White-tailed Hawk is better adapted to the Nicaraguan savanna environment than is the Red-tailed Hawk, and competition between the two may limit their relative abundance.

The two species of the genus *Falco* differ considerably in size; the Aplomado Falcon weighs about three times as much as the American Kestrel. Great disparity in size is frequent in cases of congeneric sympatry in this family (Schoener, 1965) and these two species probably compete very little, if at all.

Rusty Sparrows and Botteri's Sparrows also differ greatly in size, and I have considered this difference in relation to all six fringillids found in the pine savanna. Within a relatively similar intrafamilial group of species, meas-

TABLE 5

Pine Savanna Resident Birds grouped according to Food Habits

Species	*Habits*
	Carnivorous
Buteo albicaudatus *Buteo jamaicensis*	Potentially competitive
Falco femoralis	Large; scarce; feeds on birds?
Falco sparverius	Small; common; partly insectivorous
Polyborus cheriway	Carrion-feeder
Bubo virginianus	Large; nocturnal; rare
	Insectivorous
Chordeiles minor	High-flying, semi-nocturnal aerial feeder
Caprimulgus maculicaudus	Low-flying, nocturnal aerial feeder
Amazilia cyanocephala	Takes smallest arthropods, also nectar
Dendrocopos scalaris	Arboreal feeder; drilling, probing, gleaning
Pyrocephalus rubinus	Flycatches in pine stands
Muscivora tyrannus	Flycatches in open grass savanna
Cistothorus platensis	Restricted to marshes
Dendroica graciae	Largely restricted to foliage and small branches
Icterus chrysater	Arboreal icterid
Sturnella magna	Terrestrial icterid
	Omnivorous (seeds and/or fruits, insects)
Colinus nigrogularis	Terrestrial, scratches in litter; moderately large
Columbina minuta	Terrestrial, gleans from surface; small
Sialia sialis	Arboreal-terrestrial; slender bill used primarily for grasping
Piranga flava	Arboreal; heavy bill used for grasping and cutting
	Frugivorous-herbivorous
Ara macao *Amazona ochrocephala*	Do not feed in pine savanna
	Granivorous
Carduelis notata *Loxia curvirostra* *Ammodramus savannarum* *Aimophila rufescens* *Aimophila botterii* *Spizella passerina*	All fringillids; see Figure 10

urements of body weight, wing length, and bill length and depth should indicate general body size, extent of aerial activity, and feeding habits, respectively (Figure 11). The non-concordant variation in these morphological characters suggests differences in feeding activities that would lessen interspecific competition, and field observations support this idea: the Red Crossbill is a food specialist; the Black-headed Siskin and Chipping Sparrow seem to eat primarily the seeds of *Hypolytrum* and *Andropogon,* respectively; the Rusty Sparrow is much larger and wider ranging in its habits than either the Botteri's Sparrow or the Grasshopper Sparrow (*Ammodramus savannarum*). The Botteri's and Grasshopper Sparrows differ in size, but they were too secretive for detailed observation of their feeding behavior.

Table 6 gives mean measurements of wing length, body weight, and bill length for both sexes of a group of pine-savanna species for which I have such data. For each set of measurements, I calculated the per cent difference between the means for males and females by dividing the smaller figure by the larger and subtracting the quotient from one. The per cent differences are usually small, exceeding 10 per cent in some dimension in only three species—Ladder-backed Woodpecker, Yellow-backed Oriole, and Common Meadowlark. The oriole and meadowlark belong to the family Icteridae, in which the sexes often show great size dimorphism. In the woodpeckers, sexual dimorphism in size is not the rule, but measurements for various populations of Ladder-backed Woodpeckers given in Ridgway (1914) show that the male Ladder-backed Woodpecker is usually larger than the female. Thus, in these three species, size dimorphism is consistent with the trend in other conspecific populations.

In most savanna species, the low per cent difference between the sexes in culmen length is notable and is usually less than that shown in wing length and body weight. Only in the three most dimorphic species does this difference exceed six per cent. Schoener (1965) suggested that a ratio of larger to smaller bill length of 1.14 or more indicates a reduction of interspecific competition through the partitioning of food resources between the larger- and smaller-billed forms. Presumably, such differences in bill size between males and females of the same species would also lessen the competition between them for food.

Among the pine-savanna residents only the Ladder-backed Woodpecker shows a ratio of bill lengths between the sexes as great as 1.14. In the Yellow-backed Oriole, the ratio is 1.07, and in the Common Meadowlark, 1.08. This suggests a reduction in competition between the sexes in the woodpecker, but I have too few observations of this scarce species to evaluate the possibility. In the other savanna species, the lack of a "significant" intraspecific difference in bill length between sexes suggests that males and females must be using essentially the same food resources. If there is a meaningful degree of competition between the sexes, it may be partly responsible for the low densities of individuals in the savanna.

The scarcity of congeneric forms and the apparent minimizing of competition between resident species suggests an insular avifauna and the savanna as an ecological island. Compared to the montane pine forests of Honduras and Nicaragua, the lowland savanna has a much greater annual rainfall and a higher mean temperature, with the low extremes much higher. We might expect it to be more productive and support more bird species, as is the case with the lowland versus highland areas of tropical broad-leafed forest (Orians, 1969). Nevertheless, a number of arboreal species reside in the montane pine forest of Honduras and/or Nicaragua that are absent from the lowland pines: White-breasted Hawk (*Accipiter chionogaster*), Mountain Trogon (*Trogon mexicanus*), Common Flicker (*Colaptes auratus*), Hairy Woodpecker (*Dendrocopos villosus*), Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*), Greater Pewee (*Contopus pertinax*), Steller's Jay (*Cayanocitta stelleri*), Brown Creeper (*Certhia familiaris*), Solitary Vireo (*Vireo solitarius*), Olive Warbler (*Peucedramus taeniatus*), and Painted Redstart (*Myioborus pictus*). On the other hand, none of the arboreal residents and visitors of the lowland pine savanna is absent from the montane pines except the Aplomado Falcon, the Yellow-headed Parrot, and the Vermilion Flycatcher.

In several instances, the savanna avifauna includes close counterparts of montane species and competitive exclusion could explain the absence of at least some of these from the lowlands, but for some species this is not evident. In any case, the montane pine habitat clearly includes more bird species than the lowland pines. Some of the exclusively montane species possibly invaded the savanna at times and failed to establish themselves, but it is difficult to see why some such invasions—if they occurred—were not successful. It is also hard to understand why some of the savanna residents are not more abundant. For example, bark-gleaning is virtually unexploited except by the Grace's Warbler on the smaller upper branches and to some extent by the wintering Yellow-throated Warbler. Besides these warblers, the montane forest also includes the large Strong-billed Woodcreeper and the small Brown Creeper, both bark-gleaners and both absent from the lowland pines. No woodcreepers ever venture into the savanna from the broad-leafed forest.

The Ladder-backed Woodpecker is the only resident woodpecker in the pine savanna, and most other populations of this widespread species do not occur in coniferous forest. This small-billed form gleans and flakes off bark on small branches; it also drills in typical woodpecker fashion and gleans the dry bases of bromeliads. It is inexplicably scarce; I estimate a maximum density of less than one pair per 100 acres, and Monroe (1968) did not encounter any Ladder-backed Woodpeckers in the Honduran portion of the savanna.

The case of the Vermilion Flycatcher is similar. This species does not inhabit pines in most of its range and it is not abundant in the savanna. Yet it is the only small tyrannid resident in the lowland pines—the larger Fork-tailed Flycatcher (*Muscivora tyrannus*) is primarily a grass-savanna bird.

The Red Crossbill has no vertebrate competitors of any kind for the pine seeds; yet the crossbills are very rare. We collected six specimens and saw others on only two other occasions despite intensive searching.

When an island is inhabited by the same but fewer species of birds as are found on the mainland, the diminished interspecific competition may permit the insular populations to expand the dimensions of their niches beyond those of their mainland counterparts. I am familiar with the habits of most of the pine-savanna species in other, "mainland," parts of their ranges, and I watched for indications of niche expansion in the seemingly unsaturated savanna environment. One can consider the presence of typically "non-pine" species such as the Ladder-backed Woodpecker and the Vermilion Flycatcher as examples of niche expansion, but within the pine savanna their activities seemed the same as in any other open habitat. I did not detect any notable differences in the ecology of other species, and if any have developed, they are certainly inconspicuous.

TABLE 6

Sexual Dimorphism in Size in some Pine Savanna Residents

Species	*Sex*	*No.*	x *wing length*	*Per cent difference*	*No.*	x *body weight*	*Per cent difference*	*No.*	x *culmen from nostril*	*Per cent difference*
Falco sparverius	M	13	166.8	3.5	7	73.9	9.2	13	10.15	4.25
	F	11	172.8		5	81.3		11	10.6	
Colinus nigrogularis	M	8	89.0	<1	3	113.5	5.6	8	8.26	<1
	F	4	90.7		1	120.7		4	8.22	
Amazilia cyanocephala	M	8	56.8	3.7	3	(4.5, 4.9, 6.4)	—	9	16.7	2.9
	F	9	54.7		0			8	17.2	
Dendrocopos scalaris	M	3	85.7	1.9	3	26.1	5.4	3	14.6	12.4
	F	9	84.1		8	24.7		6	12.8	
Pyrocephalus rubinus	M	13	71.0	3.8	7	14.3	<1	13	9.84	0
	F	11	68.3		4	14.5		10	9.85	
Sialia sialis	M	17	95.7	2.3	11	29.5	2.4	17	9.5	0
	F	14	93.5		11	30.2		14	9.5	
Dendroica graciae	M	10	57.5	4.0	3	7.9	1.3	10	7.44	1.8
	F	6	55.2		2	7.8		6	7.58	
Icterus chrysater	M	4	104.2	10.4	2	60.2	13.4	4	17.3	6.65
	F	5	93.4		2	52.15		4	16.15	

TABLE 6 (Continued)

Species	*Sex*	*No.*	x *wing length*	*Per cent difference*	*No.*	x *body weight*	*Per cent difference*	*No.*	x *culmen from nostril*	*Per cent difference*
Sturnella magna	M	11	96.0	9.0	6	82.15	24	11	19.9	7.6
	F	9	87.4		5	62.9		9	18.4	
Piranga flava	M	10	88.4	2.4	4	34.45	5	12	13.23	<1
	F	7	86.3		1	32.8		6	13.35	
Carduelis notata	M	10	62.4	4.6	9	10.6	2.8	10	10.6	3.8
	F	5	59.5		6	10.3		5	10.2	
Loxia curvirostra	M	3	86.7	3.4	0	—	—	3	17.2	1.2
	F	3	83.8		3	33.3		3	17.0	
Ammodramus savannarum	M	3	54.1	3.4	3	15.3	5.9	3	7.3	4.0
	F	1	52.3		1	14.4		1	7.6	
Aimophila rufescens	M	11	68.9	7.0	7	35.8	8.7	10	10.7	1.0
	F	7	64.1		2	32.7		7	10.8	
A. botterii	M	8	55.3	1.1	3	19.5	—	8	8.3	3.6
	F	2	54.7		0	—		2	8.0	
Spizella passerina	M	8	65.9	4.4	6	11.6	4.3	8	7.35	5.2
	F	8	63.0		9	11.1		10	6.97	

All weights in grams (g); measurements in millimeters (mm).

I also watched for evidence of niche-narrowing in this tropical savanna that would permit coexistence of more species of similar morphology and habits, and again I found no clear-cut examples. One possible case of niche-narrowing, the apparent dependence of the Black-headed Siskin on *Hypolytrum* seeds, seems more an example of the simple use of one of the few abundant foods in a generally impoverished habitat than of the partitioning of resources in response to competition. I feel that the composition of the avifauna in the savanna results more from historical accident than from direct contemporary competition, a point I shall develop later.

Question 7

How do the proportions of non-passerines to passerines and suboscines to oscines differ in the two habitats and how may one interpret the differences?

As mentioned above, Klopfer and MacArthur (1960) suggested that the greater environmental stability in the tropics favors more stereotyped behavior patterns, resulting in smaller and more restricted niches that in turn lead to fewer individuals of each "stereotyped" species in a given area. On the other hand, birds with less stereotyped behavior would have larger niches and a greater ability to share more varied resources and this, in turn, would lead to more individuals of each species in a given area.

Although not explicitly stated, Klopfer and MacArthur imply that reduced niche sizes also permit more different species to inhabit a particular area. Klopfer (1962:84) subsequently made this suggestion. To support this hypothesis, they attempted to show that the behavior of a high proportion of tropical species is more stereotyped and that they have smaller niches than temperate-zone species. The authors proposed that non-aquatic non-passerines, being phylogenetically older than the passerines, must have a more limited "central nervous capacity" than the passerines. This should reduce their ability to modify their behavior in response to changing environmental conditions resulting in more restricted niches. The behavior of the phylogenetically younger passerines should be less stereotyped, leading to broader niches and greater abundance of individuals in unstable environments.

Klopfer and MacArthur further proposed that an increase in the proportion of non-passerines to passerine individuals—not necessarily species—from temperate to tropical areas would support their hypothesis of a tendency for more birds to have smaller, more restricted niches in the tropics. They selected 45 breeding bird censuses, taken in a variety of habitats from northern Canada to southern Mexico, and presented the data as the number of territorial males per 100 acres per species for both passerines and non-passerines. They used these figures to calculate for each area the ratio of passerines to non-passerines and the per cent of individuals which are non-passerines. The authors interpreted the figures as showing an increase in the proportion of non-passerines to passerines from north to south, thus supporting their hypothesis.

The figures vary greatly from area to area and it is difficult to distinguish clear trends even when plotted arithmetically on a graph. Only the last eight census areas are definitely tropical, and three are prairie habitats. There does appear to be a tendency for an increase in the "per cent of individuals which are non-passerine" from north to south, and a decrease in the number of passerine territorial males per 100 acres per species (Klopfer and MacArthur, 1960:295). However, I can find no clear indication of any regular increase toward tropical latitudes in the number of non-passerine territorial males per

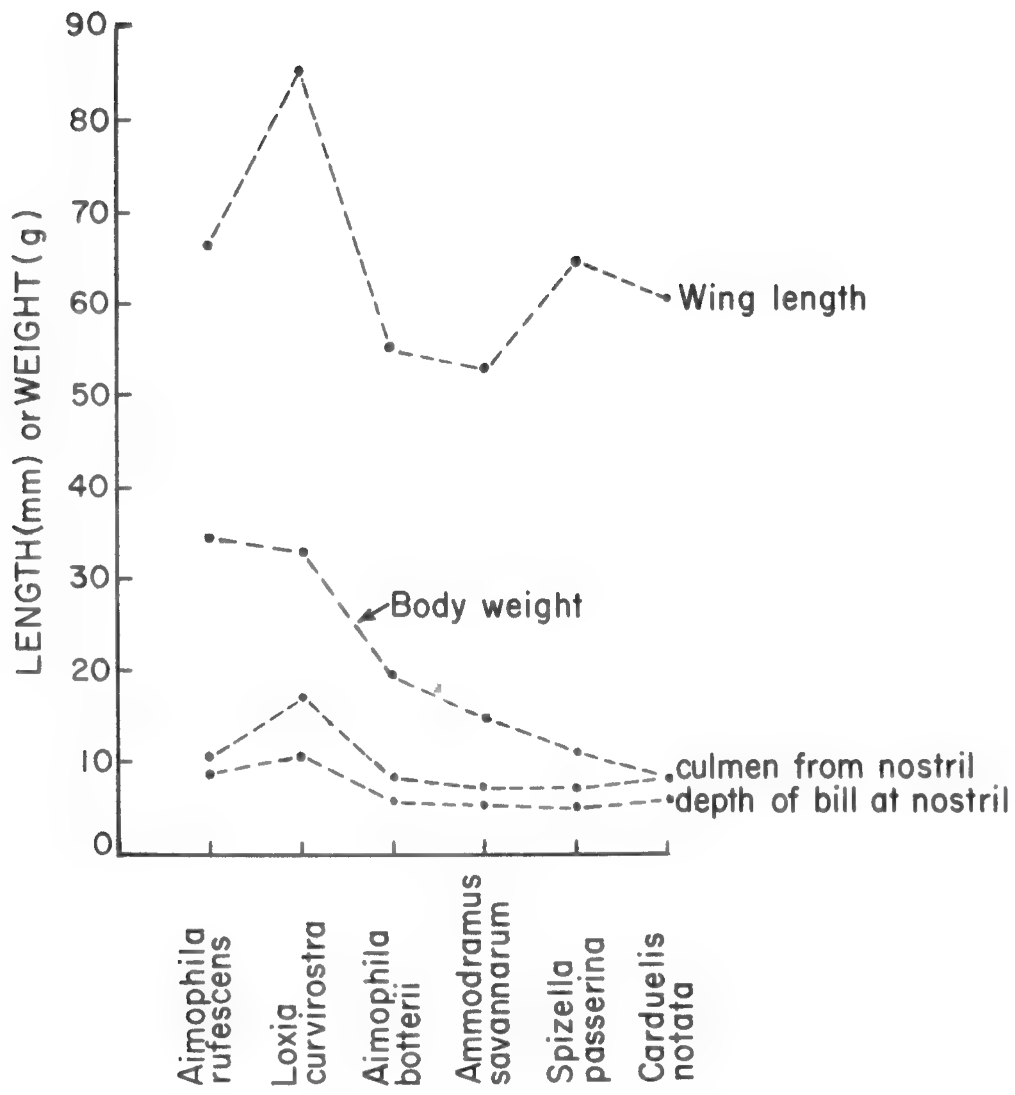

Figure 11. Body weight and measurements of pine savanna fringillids, arranged in order of decreasing body weight.

100 acres per species. This means that the increase in the proportion of non-passerines to passerines results from a decrease in the density of individuals of passerine species and not from an increase in the density of non-passerines. Therefore, the following chain of inferences is not supported by the authors' figures: (1) a higher proportion of non-passerines to passerines is found in a more stable (tropical) environment; (2) this is due to more restricted niches among non-passerines; (3) this in turn allows more species of non-passerines to inhabit a given area; (4) resulting in a greater diversity of species in the tropics. Klopfer and MacArthur (1960) rejected the possibility that tropical passerines might have more stereotyped behavior and thus smaller niches than non-tropical species as contrary to the assumption that passerines as a group have a higher order of central nervous organization and are consequently more plastic in behavior.

Even if future censuses in neotropical areas show more non-passerine territorial males per 100 acres per species than in the temperate-zone areas, I suggest that this type of census does not provide an appropriate test of Klopfer and MacArthur's hypothesis. In the approximately 15 families of non-aquatic non-passerines found in the Nearctic region, almost all the species are as large or larger than most passerines. The important exceptions are the swifts and hummingbirds (Apodiformes), especially the hummingbirds (Trochilidae). Since large non-colonial birds generally require large territories, one would expect fewer individuals of non-passerines than of passerines in a 100-acre area regardless of niche size. In the neotropics, an abundance of hummingbirds often boosts considerably the number of non-passerine species and individuals per 100 acres. The hummingbirds are adapted primarily to tropical conditions and represent the only family in which most species are smaller than most passerines.

Large, raptorial non-passerines are also more abundant and diverse in the tropics; this could be the direct result of more abundant and diverse prey types (a part of the phenomenon to be explained) rather than an indication of more restricted niches. Thus, apart from the highly questionable assumption that non-passerines are, by definition, more stereotyped behaviorally than passerines, I feel that rough comparisons of census data from very different habitats, without considering the avifaunal composition in some detail, are not meaningful.

Comparison of Pine Savanna in Georgia and Nicaragua.—I suggest that that a meaningful ecological question would be: Are individuals of bird species, particularly passerines, less abundant in tropical habitats than individuals of *similar* species in *comparable* temperate-zone areas and, if so, why? I have made such a comparison using data from the Nicaraguan pine savanna and from similar habitats in the temperate zone where the climate is less stable.

Although I did not census any single area greater than 25 acres in the pine savanna, I feel confident in estimating the bird populations that would probably occur in a 100-acre sample, based on several 25-acre censuses and all of my observations. In Table 7 I have compared my census data with Norris' (1951) extrapolated figures for 100 acres of Georgia pine forest, excluding those pairs that depended entirely on patches of broad-leafed vegetation.

The two areas have one species, five additional genera, and two more confamilial forms in common. The list of bird species shows that my study plot in Nicaragua is somewhat more open in aspect than is Norris' plot in Georgia. Nevertheless, both areas support the same number of species—15. The greater number of non-passerine species in the tropical area results from the inclusion of two open-country species, the American Kestrel and Common Nighthawk, common to both geographic regions but not occurring in the Georgia plot, and one hummingbird that feeds at flowering mistletoe and bromeliads not present in the Georgia pines.

The total number of territorial males per 100 acres per species is much higher in the temperate-zone area for both non-passerines and passerines. This is particularly striking in the passerines except for the Common Bluebird, which favors more open habitats. The higher ratio of non-passerines to passerines in the tropical area is due to the low density of individual passerines per species and not to an increase in the density of non-passerines. After allowing for the slight differences in the habitats, the data show that, even though the number of species is approximately the same, the density of individuals per species is generally much greater in the temperate area than in the tropical area. This fundamental aspect of the phenomenon of tropical diversity is worth considering in detail.

Despite my criticism of Klopfer and MacArthur (1960), I agree with one of their major proposals—that birds tend to have narrower niches in the tropics than in temperate regions, resulting in lower densities of individuals in the tropics, but irrespective of whether the birds are non-passerines or passerines.

Of the species listed for the Nicaraguan pine savanna, almost all are strictly confined to that habitat at all seasons. Few, if any, of the birds listed for the Georgia pines are so restricted. A comparison of the closely related congeneric forms common to both areas makes this clear. The Common Bobwhite in Georgia uses much more varied habitat than the Black-throated Bobwhite (*Colinus nigrogularis*) in Nicaragua; the same is true of the Downy Woodpecker (*Dendrocopos pubescens*) and Ladder-backed Woodpecker, and of the Summer Tanager (*Piranga rubra*) and Hepatic Tanager. Even species characteristic of the temperate pine woods, such as the Pine Warbler and Bachman's Sparrow (*Aimophila aestivalis*) frequently range into other habitats, especially in winter (Bent, 1953; Weston, 1965, 1968). Many of the Georgia species are migratory and occupy different habitats in winter. In the Nicaraguan list, only the Common Nighthawk is migratory. In summary, the evidence shows that the pine-dwelling birds in the temperate zone are much less restricted to this habitat than their tropical counterparts. This means that the temperate-zone birds have broader niches by any definition of the term. Having a broader niche—and the concomitant ability to use a wide variety of available resources—would not necessarily enable a species to achieve a high population density if it is confined to a habitat where the spectrum of resources is narrow and limited in quantity. We have no measure of the variety and abundance of resources available to birds in the two pine areas, but the resources are presumably greater in the temperate area, at least in spring and summer, in view of the fact that the number of breeding birds is five times greater than in the tropical pines. However, I doubt that the Georgia pines could maintain a winter population equal to that of the warm seasons.

Norris did not census his area in winter, but the two most abundant species, the Pine Warbler and Bachman's Sparrow, form winter flocks and range out into other habitats, and three other abundant breeders—the Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Wood Pewee (*Contopus virens*), and Summer Tanager—migrate to non-pine tropical areas.

Davenport (1964, 1965, 1966) censused his Georgia pine area in winter and found that about half of an average of 20 breeding species migrated out, and that the number of individuals of permanent resident species was much less in winter than in summer. Even an influx of wintering migrants did not bring the number of individuals of all species up to the level found during the summer. Clearly, the pine-dwellers in the temperate zone use their capacity for broader niche exploitation to occupy other habitats when changes of season make it advantageous.

In contrast, the bird populations in the Nicaraguan savanna change very little throughout the year. In August, the young birds increase the numbers of individuals of permanent residents, and in winter some North American migrants arrive. They compete only partly, if at all, with the residents. However, the permanent residents do not seem to change the dimensions of their niches with the seasons and many appear to remain paired and to maintain the same home ranges throughout the year. In an impoverished habitat such as the pine savanna, this leads inevitably to a wide spacing and low density of individuals.

One could propose that the environment in the Nicaraguan pine savanna with its wet and dry seasons and frequent fires is actually just as unstable and

TABLE 7

Comparison of Pineland Bird Populations

*Georgia**		*Nicaragua*	
Species	*Territorial males (pairs) per 100 acres*	*Species*	*Territorial males (pairs) per 100 acres*
	Non-Passerines		
		Falco sparverius	0.25
Colinus virginianus	5.8	*Colinus nigrogularis*	3.0
		Chordeiles minor	1.0
		Amazilia cyanocephala	3.0
Centurus carolinus	1.2		
Dendrocopos pubescens	4.7	*Dendrocopos scalaris*	0.25
Total	11.7		7.50
	Passerines		
Myiarchus crinitus	14.0	*Pyrocephalus rubinus*	0.5
Contopus virens	21.0	*Muscivora tyrannus*	0.25
Cyanocitta cristata	11.6		
Parus carolinensis	2.3		
Parus bicolor	4.7		
Sitta pusilla	9.3		
Sialia sialis	2.3	*Sialia sialis*	4.0
Polioptila caerulea	2.3		
Vireo flavifrons	2.3		
Dendroica pinus	30.3	*Dendroica graciae*	10.0
Piranga rubra	10.5	*Piranga flava*	6.0
		Icterus chrysater	0.25
		Sturnella magna	5.0
		Carduelis notata	2.0
Aimophila aestivalis	69.9	*Aimophila rufescens*	5.0
		Spizella passerina	1.0
Total	180.5		34.00
	Mean abundance; territorial males per 100 acres per species		
Non-passerines (n-p)	3.9		1.5
Passerines (p)	15.0		3.4
p/n-p	3.8		2.3

*Data from Norris, 1951.

rigorous as the environment in the Georgia areas, and that this instability causes a low diversity and low population density. However, the dry season is only relatively dry; there is usually some rain as well as permanent streams and ponds. Fires are also characteristic of the temperate pinelands, including Norris' study area in Georgia. Periodic burning is a management technique for increasing quail populations and, incidentally, those of meadowlarks and some sparrows (*Aimophila*). In fact, in habitats where fires are frequent and natural, periodic burning is not a disaster and may even help to maintain or increase bird populations, including those of ground-nesting species (Komarek, 1966; Lawrence, 1966; Stoddard, 1932). It is, therefore, improbable that the stress of fires in the Nicaraguan savanna is equivalent to the climatic stress in the temperate zone.

Thus, in two very similar habitats, the one with an equable tropical climate supports a much sparser bird population than the one with a more variable temperate climate. I attribute a large part of the difference to the use of broader niches, at different seasons, by the temperate-zone species. In the northern temperate regions, which have only become habitable for their present avifauna within the last few thousand years, selection naturally favored broad-niche species that could adapt to marked seasonal changes.

Specialization to a pine-forest environment involves a narrowing of niche dimensions. In tropical regions, where selective pressures for maintaining broad niches are slight and countered by competition with established residents in the broad-leafed forest, the narrowing could reach an extreme. This may have happened in the tropical pine savanna, where most species appear to be of northern derivation. Although this specialization to narrow niches may have reduced the numbers of individuals, it has not led to a greater diversity of species; that requires more niches.

Slud (1960) pointed out that the ratio of suboscine to oscine passerines increases from North America through Central America to the equatorial forests of South America. His interpretation is that suboscines evolved in conjunction with humid lowland tropical forests and are more numerous and diverse than oscines in such associations, but they diminish northward as that habitat diminishes in extent and complexity. The suboscine to oscine ratio also drops in open and drier habitats, even in equatorial regions, suggesting that the oscines in general may be better adapted to such environments. These phenomena may relate to the fact that suboscines are almost entirely insectivorous or frugivorous or both whereas oscines include many types that feed on hard dry seeds. In the Nicaraguan study areas, suboscines comprise most of the rain forest passerines but there were no suboscines in Pine Savanna Areas 1 and 2; the only permanent-resident suboscine species in the unmixed savanna are the Fork-tailed and Vermilion Flycatchers, and as Orians (1969) pointed out, flycatchers (tyrannids) are the most successful suboscine family in temperate environments. The savanna includes six or seven (including the Yellow Grass-finch) permanently resident species of fringillids, but in the otherwise richer Rain Forest Area we recorded only five species of fringillids, of which only the Black-faced Grosbeak and Orange-billed Sparrow spent much time inside the forest as opposed to the edge. As open and drier habitats generally include many plants with seeds that lack an edible outer covering, such habitats predictably support more seed-husking or seed-cracking species—usually oscines—than do humid forests.

Question 8

What is the ecological effect of wintering North American migrants on the resident birds in both habitats?

The influence of North American migrants on the resident avifauna of the Nicaraguan study areas appears to be negligible with one striking exception—the Yellow-throated Warbler—which I shall discuss below.

We recorded 15 North American migrants in the Rain Forest Area (Table 3)—one species each in the families Tyrannidae (assuming that the pewee, *Contopus* sp. is a migrant), Mimidae, Turdidae, Vireonidae, Icteridae, Thraupidae, and nine species in the Parulidae. Other than the Catbird (*Dumetella carolinensis*), Summer Tanager, Magnolia Warbler (*Dendroica magnolia*), and Chestnut-sided Warbler (*D. pensylvanica*), the migrants appeared to be only casual visitors. The Catbird, a thicket-inhabiting bird, is the only mimid that occurs in Nicaragua. The Summer Tanager and Chestnut-sided Warbler usually occur in the higher levels of the forest; the Magnolia Warbler may occur at all levels, but is usually less than 20 feet above ground. As most of the resident species forage at the lower levels, one might expect this warbler to encounter severe conflict with the residents, yet it was the most abundant of the North American wintering species.

None of the migrants was numerous; we seldom saw as many as three individuals in a census of the 10-acre area. I never noticed any aggression between the migrants and resident forms, and from this negative evidence I presume there is little important competition between them. Willis (1966b), in a study of interactions between migrant passerines and resident ant-following species in the rain forest on Barro Colorado Island, Panama, concluded that the migrants do not restrict the residents; rather, the residents restrict the migrants to the use of sporadically superabundant food.

In the pine savanna, we recorded only five species of winter residents (Table 1). The Yellow-bellied Sapsucker (*Sphyrapicus varius*) was scarce and we never observed it interacting with other woodpeckers. The sapsucker also ranged into the broad-leafed forest, and with its ability to feed on sap and cambium, it probably does not compete importantly with the permanent residents. We recorded the Tree Swallow (*Iridoprocne bicolor*) only in one year; this aerial feeder had no competitors over the savanna in winter.

Three species of warblers are present in winter in addition to the permanent-resident Grace's Warbler. The Palm Warbler (*Dendroica palmarum*), a ground-feeder, is scarce; the Myrtle Warbler (*D. coronata*) is common, but in this region is primarily a "flycatcher" at middle and lower levels as well as a shrub- and ground-feeder. Neither of these warblers appears to compete importantly with the Grace's Warbler. The Yellow-throated Warbler, however, feeds in trees at the same levels as the Grace's Warbler, and the two species show quite similar color patterns. Although the Yellow-throated Warbler winters in non-coniferous forest on the Pacific slope of Nicaragua, we did not observe it outside the pine savanna on the Caribbean slope and Russell (1964) listed it as common in the pines in British Honduras.

In the Nicaraguan savanna, the Yellow-throated Warbler arrives at least by mid-August and was present until late March 1966, but not in mid-April 1967. The Yellow-throated Warbler and Grace's Warbler often foraged in the same general area or in the same tree. In fact, we found the two species close together so frequently that mere coincidence seems unlikely. The Grace's Warbler often attacked the larger Yellow-throated Warbler but not *vice versa;*

the Yellow-throated Warbler usually retreated only as far as was necessary to avoid further attacks and resumed foraging.

The two are potentially competitive, but clear-cut differences in morphology and feeding behavior probably account for their successful coexistence for at least eight months of the year. The Yellow-throated Warbler is larger and has a longer bill than the Grace's Warbler. Three specimens of the Yellow-throated Warbler, collected in the Nicaraguan savanna, had a mean wing length of 64.7 mm, about 8 mm longer than the mean for the savanna population of the Grace's Warbler (Table 5). Measuring only the specimens collected in the Nicaraguan savanna, the mean culmen-from-nostril length of three Yellow-throated Warblers was 9.6 mm and the mean for 16 Grace's Warblers, 7.5 mm, giving a ratio of 1.28, well above the ratio of 1.14 suggested by Schoener (1965) as the minimum ratio indicative of partitioning of food resources by their size or dimensions.

TABLE 8

Shared Taxa of Birds in three Different Latitudinal and Ecological Areas

Family	*Genus / Species*	*Vermont (temperate deciduous woodland)*	*Georgia (Pine forest)*	*Nicaragua (Pine savanna)*
Picidae	*Dendrocopos*	X	X	X
Sittidae	*Sitta*	X	X	
Turdidae	*Sialia sialis*		X	X
Vireonidae	*Vireo*	X	X	
Parulidae	*Dendroica*	X	X	X
Thraupidae	*Piranga*		X	X
Fringillidae	*Aimophila*		X	X

There is some overlap in their foraging activities in that both species worked over the branches and foliage of the pines and did some flycatching; there were also well-marked differences. Most of the time, the Grace's Warbler moved out from the tree trunk along the upper surface of small branches of larger trees, taking food from the bark and then gleaning the bases of the needle clusters. It usually foraged on branches that did not exceed, roughly, the diameter of its own body, enabling it to reach around most of the branch with its bill without having to hang upside down. On the few occasions when we saw Grace's Warblers foraging on large branches, they seemed able to cling only momentarily to the undersides before falling away. The Grace's Warbler very seldom foraged on tree trunks, but frequently sallied after flying insects and captured some as large as small dragonflies (Odonata).

In the Nicaraguan savanna, the Yellow-throated Warbler exploits the bark-gleaning niche that appears largely unfilled by any resident species. Unlike the Grace's Warbler, the Yellow-throated often frequents the larger branches and tree trunks, where it reaches into crevices with its long, slender bill. It moves over vertical trunks and along the underside of branches in much the same manner as the Black-and-white Warbler (*Mniotilta varia*), a species that winters in the adjacent broad-leafed forest but almost never ventures into the pines.

A comparable situation exists in the pine forests in the southern United States where Ficken *et al.* (1968) studied competition between the Yellow-throated Warbler and the Pine Warbler. The ratio of the bill lengths of Yellow-throated Warbler/Pine Warbler is 1.24—very close to that shown for Yellow-throated Warbler/Grace's Warbler in Nicaragua. The population of Yellow-throated Warblers studied by Ficken *et al.* used the longer bill in probing cones of *Pinus taeda,* one of the three species of pines present; they did not see the Pine Warbler probe cones and showed that its bill and skull morphology would make this activity ineffective. In the Nicaraguan pines, we never saw either warbler probe cones, but the longer bill of the Yellow-throated Warbler allows it to probe into deeper bark crevices and exploit a food source unavailable to the Grace's Warbler. Whether or not the Yellow-throated and Grace's Warbler could coexist as breeding species, particularly in an area with only one species of pine, is a moot question. In April, when the Yellow-throated Warbler was absent, the Grace's Warbler appeared to explore the bark crevices of the larger branches and trunks more often, but it seemed poorly adapted for this type of feeding. It also foraged frequently among the small pines and seedlings, but did not seem to obtain much food from them.

In summary, the evidence suggests that the Yellow-throated Warbler during its winter residency exploits a foraging mode that is not used in the savanna during the breeding season. I doubt that the presence of the Yellow-throated Warbler lowers the population density of the Grace's Warbler but we need more data to be certain.

Question 9

What historical factors may have been responsible for the difference in the avifauna of the two habitats?

Although one cannot entirely separate the influences of historical from ecological factors in determining the composition of the avifaunas of the savanna and rain forest areas, distinctions are possible. Given the same contemporary ecological conditions, a different history might have produced different avifaunas.

The rain forest of the Caribbean slope of Nicaragua probably has been essentially continuous with that of Costa Rica, Panama, and much of South America since the end of the Pliocene period. The bird species are mostly of tropical affinity, and the varied composition of the avifauna is not surprising.

The Nicaraguan pine savanna is probably of relatively recent origin. It may be no older than the cut-and-burn agricultural practices of the aboriginal Indians; or, it may date back to the last glacial period which presumably caused the pine forest to extend into tropical latitudes. A reasonable guess is that the age of the Nicaraguan pine savanna is between 1,000 and 10,000 years.

The length of time that the lowland pine savanna has been isolated from other pine-forest habitats—assuming that some connection once existed—must be less than the age of the pine-savanna habitat as such. The presence of well marked subspecies of birds representing several different orders and families indicates a high degree of isolation (Howell, 1965; Monroe and Howell, 1966; Monroe, 1968).

The Nicaraguan pine savanna represents a relatively recent, terminal, and isolated segment in the tropics of a specialized habitat that is more characteristic of high-latitude regions; one would expect its avifauna to include a depauperate sample of primarily temperate-zone species adapted to a temperate-zone environment, and to lack many other potentially successful adaptive types. I suggest that the absence of many of the potentially adaptive types is a consequence of historical accident and not of ecological unsuitability; other actually or potentially pine-adapted species have simply not reached the area, or have not reached it in sufficient numbers at the right season, to establish themselves. If the tropical conditions of the lowland pines were generally unfavorable to species derived from the north-temperate zone, one would not expect to find the Red Crossbill and Chipping Sparrow. On the other hand, species of the humid lowland forest have always had ample opportunity to occupy the pines, but none has succesfully or completely taken this step.

Of the permanent-resident pine-savanna species that are probably not of temperate-zone origin, the only tropical forms we find in the savanna are those that are adapted elsewhere in their ranges to open and sometimes arid or semi-arid habitats. This fact again emphasizes the recency of the habitat, for several species of the humid forest edge that frequently use open vegetational associations are only visitors to the savanna despite the apparently vacant niches.

The apparent trend is that birds of tropical affinity are gradually invading the savanna while pine-savanna birds are not invading the broad-leafed forest. Even such a versatile form as the American Kestrel has not yet begun to occupy the numerous clearings in the broad-leafed forest that seem to offer suitable foraging conditions and no obvious competitors. In this meeting of characteristically temperate-zone and tropical-zone habitats, there is no evidence of general adaptive superiority of species of temperate-zone origin.

In summary, the sharp ecological differences between the pine savanna and rain forest environments account in the main for their avifaunal differences, but historical factors—the antiquity and continuity of the rain forest and the recency and isolation of the pine savanna—are probably responsible for many important details in the composition of their avifaunas.

Latitudinal Gradients and Species Diversity

Question 10

What relevance do the answers to these questions have to the subject of latitudinal gradients in bird species diversity?

When I began this study in 1965, one of my objectives was to contribute to the understanding of latitudinal gradients in species diversity. Since that time, the theoretical question of why there are such gradients has been beaten, if not to death, at least to the point of greatly reduced viability. Two recent symposia (Lowe-McConnell, 1969; Brookhaven Symposia in Biology Number 22, 1969) include numerous sophisticated mathematical models and brilliant analogies that deal with many aspects of tropical diversity. The conclusions that I reached from my data include some that are very close to those of Slobodkin and Sanders (1969) in their contribution to the latter symposium, and in such instances I will frequently paraphrase and use terms from their excellent and lucid review, without pretense of originality. Actually, many of the ideas supported by those authors are virtually traditional, but are worth reiterating as they are often doubted or denied.

My data from the rain forest study area confirm as expected that this type of habitat supports a greater diversity of bird species than does temperate forest, but also show that the diversity is much greater than that predicted from a foliage profile based on three or even five layers. Either the hypothesis that bird species diversity can be predicted from foliage profile is insufficient, or the vegetation measurement and bird censusing techniques are inadequate for the complex tropical rain forest. Predictable or not, the high diversity figure merits closer examination.

In avian taxonomy, the families are generally less broadly inclusive than those in other classes of vertebrates and tend to comprise very similar adaptive types. Members of many avian families are therefore likely to be readily recognizable variations on an ancestral adaptive theme, and the theme may be identifiable as to its probable region of origin. An adaptive pattern that importantly involves sallying after flying insects or feeding on nectar almost certainly evolved in the tropics, where these food resources are available the year round. In contrast, a pattern that often includes high resistance to cold, opportunistic foraging modes, and even storage and recovery of seasonally abundant food is likely to have evolved in high latitude regions. Thus, although avian families may be rather finely split taxonomically, the family thereby gains in usefulness in tracing evolutionary histories.

An analysis of the distribution of birds in Central America (Howell, 1969) shows that, in some families, the number of species decreases from temperate to tropical regions whereas in other families the reverse is true. For example, the Corvidae (ravens, crows, jays) and the Paridae (chickadees, tits) show greater species diversity in the temperate zone than in the tropics, and the Trochilidae (hummingbirds) and the Tyrannidae (New World flycatchers) show the opposite trend in diversity. The families Corvidae and Paridae probably originated in the temperate zone, and the hummingbird and flycatcher families probably arose in the tropics. Some taxa in each of these families have successfully colonized habitats in climatic zones other than the one in which the group probably originated, but the overall tendency is for a lessening of species diversity from the environment of probable origin toward its periphery. Although groups adapted to temperate zone conditions tend to decrease or increase in species diversity with decreasing or increasing latitude, respectively, the number of species in the tropical-adapted groups is so much greater that their increase or decrease completely overshadows the trend of the temperate zone groups. If one considers only the total number of species in each of a series of regions, the conclusion is that the class Aves shows increasing species diversity with increasing latitude, but this is a composite of opposing trends.

A basic question, therefore, is: "Why are there so many species in tropical-adapted avian groups?" I assume that rates and mechanisms of speciation are adequate to produce at least as many species as the environment can support in both temperate and tropical forests, and the question pertains to the factors that make possible the continued existence of such large numbers of species in the latter habitat. A frequently offered answer is that there are more and perhaps narrower niches in the tropics, but as Slobodkin and Sanders (1969) point out, this type of argument is circular even if the statement is true. As we recognize and define niches by the presence of occupying species, many species must mean many niches. However, few species could mean either fewer niches, or some unoccupied niches, or larger niches for fewer but more broadly adapted species. If there are more and narrower niches in the tropics than in the temperate zone, one must explain why there are more, and why there are so many different species occupying them.

Slobodkin and Sanders (1969) discussed species diversity in terms of severity and predictability of environments. By a "predictable" environment they mean one in which the variances of environmental properties around their mean values are relatively low and predictable, both spatially and temporally. Severity of conditions leads to low diversity, but given predictability of conditions many kinds of animals can adapt physiologically or behaviorally and persist. Coping with unpredictable conditions requires a broader range of adaptation, and species that lack that capacity will be eliminated; even fewer can survive conditions both unpredictable and severe. The latter type of environment should have the lowest diversity of species, and a predictable and benign environment should have the highest diversity. The tropical rain forest approximates such an environment as it is highly predictable and lacks extremes of temperature and aridity. Applying these concepts to birds, one may summarize as follows:

1. In the New World equatorial regions, the predictable and benign humid lowland forest has existed in varying extent for the duration of the evolutionary history of birds.

2. In this habitat, many species may persist—even if rare—that could not survive in unpredictable and severe conditions characteristic of higher-latitude environments. The humid tropical forest not only supports broad-niche species but tends to accumulate a variety of narrow-niche specialists. The latter are often sparsely distributed but so well-adapted to their microhabitats that they are able to maintain themselves in competition with invading or newly-evolved jack-of-all-trades species.

3. In the less predictable and often severe temperate zone, narrow-niche specialists may also invade or evolve, but if dependent on a few critical conditions or resources that disappear with drastic climatic change—seasonal or through geologic time—such species will be eliminated. Unpredictable conditions also favor the evolution of broadly-adapted forms.

4. Humid tropical forests thus support a great number of bird species, many with low population densities, occupying a great variety of niches. In the temperate zone and higher latitude regions, relatively few but broadly-adapted species partition the environmental resources. When such resources are abundant, partitioning by relatively few species leads to large numbers of individuals of each.

A frequent criticism of such proposals is that they fail to account for the great diversity of tropical plant species required for the great variety of niches, thus begging the question or merely pushing it back one step. However, the same reasoning that may explain diversity of animal species seems equally applicable to diversity of plant species, and Janzen (1970) has shown that, in the tropics, heavy predation on seeds and seedlings near the parent plant may account for the absence of pure stands, and consequently the greatly mixed distribution of plant species in tropical forests.

The Nicaraguan pine savanna is virtually as predictable as the adjacent rain forest but is less benign. There is much less shade, evaporation rates are higher, the soil is leached and poorer in organic nutrients, and there are extensive fires in the dry season. This periodic burning may not be detrimental to pine- and grassland-adapted birds, but it certainly constitutes severe physical stress for many plants, insects, and other invertebrates and possibly for some reptiles and small mammals. It definitely limits invasion of the savanna by many broad-leafed plant species and thus restricts the variety of possible niches there; in Slobodkin and Sanders' terms, the pine savanna lacks the geometrical complexity and spatial heterogeneity of the rain forest.

Paine (1966) showed that predation on invertebrates in the rocky-intertidal zone favored species diversity by preventing the monopoly of resources by one or a few species, and proposed that predation is a generally important influence on species diversity. MacArthur (1969) used similar reasoning in suggesting that high predation in the tropics leads to high species diversity there. The Nicaraguan savanna avifauna includes a higher proportion of predatory birds than does the adjacent rain forest or temperate pinelands, but bird species diversity is low. Possibly most of the raptors in the savanna do not feed primarily on birds, but some do in part. Other potential predators on birds such as snakes and carnivorous mammals appear to be extremely scarce in the savanna, and Paine's and MacArthur's proposals may be valid for other habitats where such types are abundant.

The sparse avifauna of the tropical pine savanna at first seems to contradict the principle that predictable and relatively benign habitats will have greater species diversity than less predictable and more severe habitats, for temperate zone pinelands are in the latter category but support breeding bird faunas at least as diverse as in the tropical pines and have greater numbers of individuals. I attribute the relatively low population density of the pine savanna birds in part to the fact that most of them do not or cannot invade the adjacent broad-leafed forest and use the more abundant resources there. As previously mentioned, the equivalent temperate pineland birds often range into other habitats, at least seasonally. Thus, the dimensions of the niches of many of the tropical pine savanna birds are narrower, but narrower niches alone have not brought about greater species diversity. The Nicaraguan pine savanna is also relatively recent in age and lies at the periphery of this type of habitat; given enough time, more species of pine-adapted or open-country birds might reach the savanna and establish themselves. It is also possible that, for the same reasons, potential foods for birds are presently scarce there and might ultimately increase. Thus, in the Nicaraguan savanna, the conditions usually associated with low latitudes—predictable and benign climate, low population densities and narrow niches of resident bird species—are as yet insufficient to bring about high species diversity because of the low variety of niches and the isolation from the pool of species potentially able to establish themselves there.

Even if the savanna were not a recent formation, however, I do not believe it could ever approach the high species diversity of the adjacent rain forest. The rain forest habitat has varied resources for nectar, fruit, and insect eaters, and a highly varied foliage physiognomy. Its bird population is primarily derived from groups of tropical South American origin and descendants of the pre-Pleistocene avifauna of tropical North and Central America. Recurrent periods of aridity in the Pleistocene isolated segments of humid lowland forest and this probably augmented the differentiation of many similar forest-adapted tropical bird species, especially in South America (Haffer, 1969). Some of these have doubtless extended their ranges north through the now continuous rain forest of the Caribbean slope, at least part of which has probably existed throughout the Cenozoic era.

Pleistocene glaciation in North America forced the ranges of many species far to the South and eliminated others, leaving an avifauna largely of temperate-adapted types including those specialized for exploitation of coniferous forests and grasslands. The Nicaraguan savanna represents the southernmost extent ever reached in the New World by the pinelands habitat, and its bird species are largely of temperate zone origin and constitute a depauperate sample of the avifauna of the temperate pinelands that has reached tropical latitudes primarily at high elevations. The few bird species of probable tropical origin that have colonized the lowland pine savanna are not fully pine-adapted; they only take advantage of its open aspect, or obtain food from tropical epiphytes. In a sense, the pine savanna represents the worst of two worlds—too recent and too remote for colonization by most temperate pine-adapted birds, and too austere ecologically for most tropical forest birds.

All this leads to the scarcely original but common-sense conclusion that high species diversity depends on a constellation of conditions that are most likely but not invariably to be found at tropical latitudes, and when one or more of these conditions is absent—as is likely in higher latitudes—species diversity declines. I have discussed some of these conditions previously and I cannot hope to recognize and list all the possible ones. Probably the influential factors vary with the case under scrutiny, and we may never achieve a general and comprehensive theory to account for all gradients in species diversity. As MacArthur (1969) points out "... statistical events like species diversity often have complex and multiple explanations. Hence, there is no reason that the validity of any of the [possible] explanations need preclude any of the others."

For the situations I have tried to analyze, there are certainly multiple explanations. In addition, at least among Central American birds, there are opposing gradients of species diversity in groups of temperate and tropical origin where temperate environments extend into tropical latitudes and interdigitate with attenuated tropical environments. Lumping the total number of species found at a given latitude gives the misleading impression of a relatively uniform gradient of increasing species diversity from north to south. Therefore, in attempting to explain gradients in bird species diversity, one must consider not only a wide range of ecological parameters but also the geologic history of the region in question and the distributional and evolutionary history of the species under study. The same precaution may prove fruitful in analyzing the species diversity patterns of other organisms as well.

Summary

I used the method of MacArthur and MacArthur (1961) to measure the vegetation density at three levels in two areas of pine savanna and one area of rain forest, and I calculated foliage profiles and foliage height diversities (FHD) for each area. I have described the methods in detail. From censuses of birds in the three areas made at different times of the year, I calculated resident bird species diversity (BSD) and compared these results with the figures predicted by the equation $\text{BSD} = 2.01\ \text{FHD} + .46$, derived from temperate-zone data by MacArthur and MacArthur (1961).

Bird species diversity in one savanna area with sparse seedlings and shrubs approximated the predicted value only when it included 25 acres instead of the five used in the temperate-zone study. In a second savanna area with numerous seedlings, the FHD was greater but the observed BSD was lower

than that predicted from it. This suggests that the seedling layer eliminated some bird species but added none. When the area was treated as a two-layered habitat, the predicted BSD and the observed value were much closer. In the rain forest area the observed BSD was much greater than that predicted from the FHD even when the latter was calculated from five instead of three layers of vegetation.

A census of a five-acre grassland in the savanna in April yielded no nesting birds although grassland species were then in breeding condition. This result indicates low population densities and patchy distribution of grass-dwelling birds.

I compare my results with data from temperate-zone forests, both deciduous and pine, and discuss the possible influences of competition, niche size, and related ecological and historical factors on bird species diversity. I conclude that the avifaunas of the pine savanna and adjacent rain forest are almost totally different, largely because of different adaptations and distributional histories, and that there are fewer niches for birds in the pines than in the adjacent rain forest. As expected, the tropical rain forest area has a greater number of bird species but fewer individuals per species than have temperate-zone forest areas of comparable size. I attribute this to the greater variety of niches for birds in the tropical forest, many of which are occupied by narrow-niche specialists that can persist under mild and equable conditions but could not survive more rigorous temperate-zone conditions and the competition from species well-adapted to them. Unexpectedly, the tropical pine savanna area has no greater species diversity and has lower densities of individuals than have temperate pineland areas of comparable size. From the data on the pine savanna, I conclude that: (1) in similar habitats, at different latitudes, a more predictable and benign climate does not necessarily result in an increase in the number of bird species or of individuals; (2) some bird species in tropical areas have a smaller range of foraging activities and habitat usage than their temperate zone equivalents, but this does not necessarily lead to greater species diversity although it may result in a lower density of individuals; (3) bird species diversity varies in different groups in different habitats at the same latitude—for example, diversity of fringillid species is greater in the pine savanna than in the rain forest, whereas suboscine passerines show a much greater diversity in the latter habitat; lumping all bird species at a given latitude into a single total conceals such distinctions; (4) the geological history of the Central American region and the evolutionary history of its bird life have influenced the avifaunal differences between the pine savanna and adjacent rain forest and also the nature of the latitudinal gradient in bird species diversity.

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APPENDIX 1

Method Used in Obtaining Foliage Height Diversity (FHD) and Bird Species Diversity (BSD)

Within each study area we marked 20 random points by using a table of random numbers for distances along two coordinates of a quadrilateral, and for each of these points we selected a compass direction, from 0 to 360, also from the table of random numbers. We took a white board, 30 by 30 inches, to each point and then moved either the board or the observer in the compass direction until the board appeared half-covered with foliage. The vegetation density is inversely proportional to the distance between the observer and the board; that is, the greater the distance, the less dense the vegetation. Assuming a random distribution of leaves, we express the vegetation density as $K = \frac{\log_e 2}{D}$ where K is the area of leaf surface/volume of space and D is the distance between the observer and the board, when the board appears half obscured by vegetation.

We repeated this measuring procedure for each of the 20 points for three different levels above ground and averaged the figures for each level. The number and vertical extent of the levels are necessarily arbitrary. We chose three, with dimensions that correspond roughly to a low layer of grasses and herbs, an intermediate layer of shrubs and seedlings, and a high layer of the crowns of the larger trees. One then plots the mean density figures for each level against the height to form the foliage profile (Figure 4). The maximum height on the graph is the average height of a group of randomly chosen trees that are higher than the upper limit of the intermediate layer. If the investigator delimits the levels appropriately, the foliage profile should agree with his subjective impression of the vegetation of the area.

Using data on vegetation density in the different layers, MacArthur calculated foliage height diversity (FHD) using Shannon's function $\text{FHD} = -\sum_{i=1}^{S} p_i \log_e p_i$ where S represents the number of layers of vegetation measured, and p_i the proportion of the total vegetation density represented by the *i*th layer. The figure approaches a maximum when the layers approach equal density, declines when the distribution of foliage is more unequal, and reaches zero if only one layer is present ($\log_e 1 = 0$).

The same formula provides a measure of bird species diversity (BSD) when S equals the number of bird species in an area and p_i equals the proportion of the total number of birds, or of breeding pairs, present that are represented by the *i*th species. A maximum diversity figure is approached when there are many breeding species present in equal numbers, and diversity equals zero if only one species is present. For examples and discussion of the use of this equation as a measure of diversity, see Lloyd and Ghelardi (1964), MacArthur (1964), Pianka (1966), McIntosh (1967), and Lloyd *et al.* (1968).

The size of MacArthur's study areas was at first five acres, a reasonable size for an accurate census and one that permits comparison with other census data which are often obtained in five acres or multiples of five. In later work, in habitats that had sparse bird populations, MacArthur compared census plots that included 20 to 25 pairs of birds regardless of acreage.

MacArthur and MacArthur (1961) found that, in a number of temperate-zone habitats, a plot of FHD against BSD yielded a series of points clustered about a straight line. Consideration of plant species diversity in relation to BSD did not reduce scatter of points or provide a better fit by a straight line. From this the authors concluded that, at least in the habitats they studied, they could predict the BSD from the FHD without considering the species composition of the vegetation. Their equation is $\text{BSD} = 2.01\ \text{FHD} + .46$. However, MacArthur (1964) pointed out that, in some special habitats and with some bird species that are food specialists, the proposed relationship between FHD and BSD might not hold.

We measured the vegetation characteristics of two pine savanna areas and one rain forest area by MacArthur's method with the following specifications and modifications:

1. We kept the white board, 30 by 30 inches, at the random points and the observer moved away from it.

2. We delimited three vegetation layers—0 to 3 ft, 3 to 20 ft, and 20 ft to the average height of trees over 25 ft. We selected these limits primarily on the basis of the characteristics of the savanna; the densest grass and sedge growth in the study area seldom exceeded 3 ft, and the lowest branches of the mature pines were usually about 20 or 25 ft; this left an intermediate layer between 3 and 20 ft. We could not distinguish a similarly "natural" division in the rain forest, but since no other spacing of layers seemed any better, we used the same divisions. We held the board at the following levels for measurements: 0 to 3 ft—one edge resting on the ground; 3 to 20 ft—approximately 6 ft above ground; 20 ft and above—atop a 24-foot aluminum pole.

3. For determinations above 20 ft, the observer either climbed a tree or used a ladder. When he could use neither of these methods, he backed away and estimated from the ground which foliage cluster, alone or in combination, would half obscure the board and then measured the distance from the board to this cluster. In the pine savanna, above 20 ft, sometimes only one or two foliage clumps intervened between the observer and the board. When the closest foliage clump covered less than half the board and this, combined with the second, covered more than half, we used the following calculation of foliage density:

$$\tfrac{1}{2}\,(\log_e(1 - p_1))\,/d_1 + (\log_e(1 - p_2))\,/d_2 = K$$

p_1 = proportion of board covered by first clump; d_1 = distance to first clump; p_2 = proportion covered by two clumps combined; d_2 = distance from point to second clump.

4. There was very little foliage in the intermediate layer in one of the savanna areas; sometimes the trunk of only one pine intervened between the observer and the board without half covering it or there were numerous straight trunks that covered no part of it. Feeling that we were missing 17 feet of vertical tree trunk, an important vegetational component, we made additional measurements to take this into account.

Using a forester's wedge prism with a basal area factor (BAF) of 10 at each random point, we recorded the number of trees whose trunks appeared displaced to the side by an amount less than the apparent trunk width, measured the circumference of these trees, and calculated the bark surface of that part of their trunks within the intermediate layer. We combined these figures with those for the vegetation density based on area of leaf surface when constructing the foliage profile.

5. The dense foliage of the rain forest above 20 ft sometimes completely obscured the board for an observer only a short distance away. Trial and error testing in comparably dense foliage at eye level indicated that 30 inches was a reasonable figure for the mean distance at which the board would be half obscured. Thus, for such points we assumed that D equalled 30 in.

We censused all study areas repeatedly for birds during each visit with the exception of the grassland area which we censused only twice, both times in April. One or two observers began before, or shortly after, sunrise to record species seen or heard within the area. In the pine savanna, the observer usually started at one corner, walked along one edge to the opposite corner, moved up one side a few meters, and then walked back parallel to his first crossing. By repeated crossings he could census a 25-acre area in about one and one-half hours.

We used a different method in the rain forest area where there were no obvious or recent trails. We first cut a trail around the area by following compass lines and then a random pattern of trails through it, trying to strike a balance between penetrating the densest parts and keeping the disturbance of the vegetation to a minimum. Some measure of our success, by human standards, is the fact that we often became disoriented within the 10-acre plot even after we believed we were familiar with the trails.

We censused the grassland area first on 22 April by walking back and forth across it as in the pine savanna. On 25 April, two of us dragged an 80-foot rope, stretched between us, across the entire area. Since neither method yielded a single bird, we concluded that no species nested in the grassland plot, nor used it importantly at that time of year.

We made censuses from dusk up to 18:00 or 20:00 hours several times in one pine savanna and twice in the rain forest area during April 1967. In the savanna we found no birds except the Common Nighthawk (*Chordeiles minor*) overhead. We also recorded this species in the daytime. We heard no owls and our repeated attempts to call up or eyeshine owls were unsuccessful. We detected no nocturnal birds in the rain forest area although we collected a Mottled Owl (*Ciccaba virgata*) nearby and heard, but did not identify, another owl of medium to large size just outside the area.

APPENDIX 2

Conspicuous Plants of the Savanna Study Areas and Their Importance to the Bird Fauna

Trees

Pinus caribaea, Pinaceae; most abundant tree; used to some extent, at least, by almost all savanna birds.

Curatella americana, Dilleniaceae; low and spreading, often less than 2 meters high; indicator of burned-over conditions; abundant; seldom used by birds except for perching; Yellow-bellied Sapsucker (*Sphyrapicus varius*) workings noted occasionally.

Xylopia frutescens, Ammonaceae; a few examples, less than 2 m in height, of this broad-leafed forest tree in wet areas; no use by birds observed in this early growth stage.

Shrubs

Byrsonima crassifolia, Malpighiaceae; usually less than 0.5 m high, but small tree size at edges of broad-leafed forest; large berries eaten by many birds.

Miconia lundelli; M. albidea, M. scorpioides, M. impetularis, Melastomaceae; listed in order of increasing size, about 0.5 m to as much as 2 m, and decreasing abundance; all, especially the first two, important sources of berries eaten by birds.

Palicourea guineense, Rubiaceae; up to 2 m high, found in savanna only near edge of broad-leafed forest; red flower clusters used by hummingbirds.

Sabal sp., Palmaceae; palmetto, usually in dense clumps at edge of wet areas; important cover for sparrows, particularly Botteri's Sparrow (*Aimophila botterii*).

Herbs

Tibouchina belizensis, Melastomaceae; abundant; may be 2 m high; sometimes in dense stands; provides some cover; no observed use of seeds by birds.

Clidemia rubra, Melastomaceae; abundant; less than 1 m high; no observed use by birds for cover or food.

Polygala sp., Polygalaceae; *Borreria suaveolens, Diodia frutescens,* Rubiaceae; *Cassia diphylla,* Leguminosae; all abundant, usually less than 0.3 m high, of scattered distribution; no observed use by birds.

Grasses and Sedges

Tripsacum sp., Gramineae; cane-grass, dense stands 1.5 to 2 m high in wet places, especially edges of broad-leafed forest; provides cover; seeds eaten by birds.

Paspalum humboldtianum, Gramineae; most abundant grass, almost everywhere in dense clumps up to one m high; provides cover; seeds small, no observed use by birds.

Panicum sp., *Aristida* sp., Gramineae; wiry grasses; both abundant, mixed with *Paspalum,* but smaller—usually not over 0.5 m high; provide cover; no observed use of seeds by birds.

Andropogon sp., Gramineae; broom-sedge grass; less abundant than other grasses; up to one m high; usually at edges of roads, trails, and other cleared areas; provides cover and seeds; seeds used especially by Chipping Sparrows *Spizella passerina.*

Hypolytrum schraderianum, Cyperaceae; abundant; often in dense stands, up to 1.5 m high but usually lower; provides cover; fruiting heads present at all seasons; seeds appear to be principal food of Black-headed Siskin (*Carduelis notata*), probably important to other fringillids, especially Rusty Sparrows (*Aimophila rufescens*).

Rhynchospora barbata, Bulbostylis paradoxa, Fimbristylis sp., Cyperaceae; abundant; usually less than 0.5 m high; provide cover, no observed use of seeds by birds.

Arboreal Plants

Psittacanthus mayanus, Loranthaceae; a mistletoe, fairly common in pines; red flowers in March-April, used by Red-billed Azurecrown (*Amazilia cyanocephala*); berries in August, eaten by pigeons (*Columba* sp.), probably by other birds.

Aechmea bracteata, Bromeliaceae; fairly common in pines; up to 0.6 m in diameter, holds much water and plant debris; fauna includes large ants, mosquitoes and other insects, frogs (*Hyla staufferi*); many birds probe into these bromeliads, possibly for both water and food; flowering stalks used by Red-billed Azurecrown.

Tillandsia sp., Bromeliaceae; abundant in pines; smaller than *Aechmea,* usually less than 0.25 m in diameter, but often with similar fauna; visited by many birds, but apparently especially important to Ladder-backed Woodpecker (*Dendrocopos scalaris*) which probes and gleans them.

Ferns

Blechnum sp., Blechnaceae; sword fern; sometimes abundant in wet places, absent elsewhere; no observed use by birds, but must provide some cover.

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EGG-PECKING BEHAVIOR IN GALAPAGOS MOCKINGBIRDS

ROBERT I. BOWMAN AND ANNE CARTER

Photographs by the authors

The mockingbirds of the Galapagos Islands are less well known than the classical Darwin's finches. These endemic mimids of the genus *Nesomimus* (Ridgway, 1896) attracted the attention of Charles Darwin in 1835 when he observed that on each of the principal islands, visited by H.M.S. "Beagle," dwelled a peculiar form of "mocking-thrush" (Darwin, 1845). Aside from this significant fact of zoogeography, the literature recorded little else about Galapagos mockingbirds until the close of the nineteenth century when several extensive collections of study skins were assembled for systematic studies (Ridgway, 1896; Rothschild and Hartert, 1899, 1902; Salvin, 1876; Snodgrass and Heller, 1904; Swarth, 1931).

Mockingbirds reside on almost all of the main islands except Duncan Island (Figure 1). The most modern monographer of Galapagos mockingbirds (Swarth, 1931) recognized four species: *Nesomimus macdonaldi* on Hood and Gardner-near-Hood Islands, *N. trifasciatus* formerly on Charles, but presently only on Champion and Gardner-near-Charles Islands, *N. melanotis* on Chatham Island, and *N. parvulus* on the remainder of the principal islands. *N. parvulus* is highly variable in length of bill (Figure 2) and plumage characters, with seven recognizable island races (Table 1).

Davis and Miller (1960) considered all island populations members of one species, *N. trifasciatus,* but they were probably in error. Working primarily with study skins, it is likely that they were overly influenced by Swarth's statement (1931:106) concerning the intergradation of morphological characters from form to form and largely ignored his later comment that ". . . there are gaps between certain of the forms that render it perfectly reasonable to recognize them as distinct species, though closely related and distinguished by the different extent of development of the same characters."

In recent decades ornithologists redirected their interest in Galapagos mockingbirds from the structure and form and distribution to behavioral phenomena of the living bird in nature (Beebe, 1924; Dunson, 1970; Harris, 1968; Hatch, 1965, 1966; Venables, 1940). Their findings tend to substantiate the taxonomic opinions of Swarth (1931), summarized in Table 2.

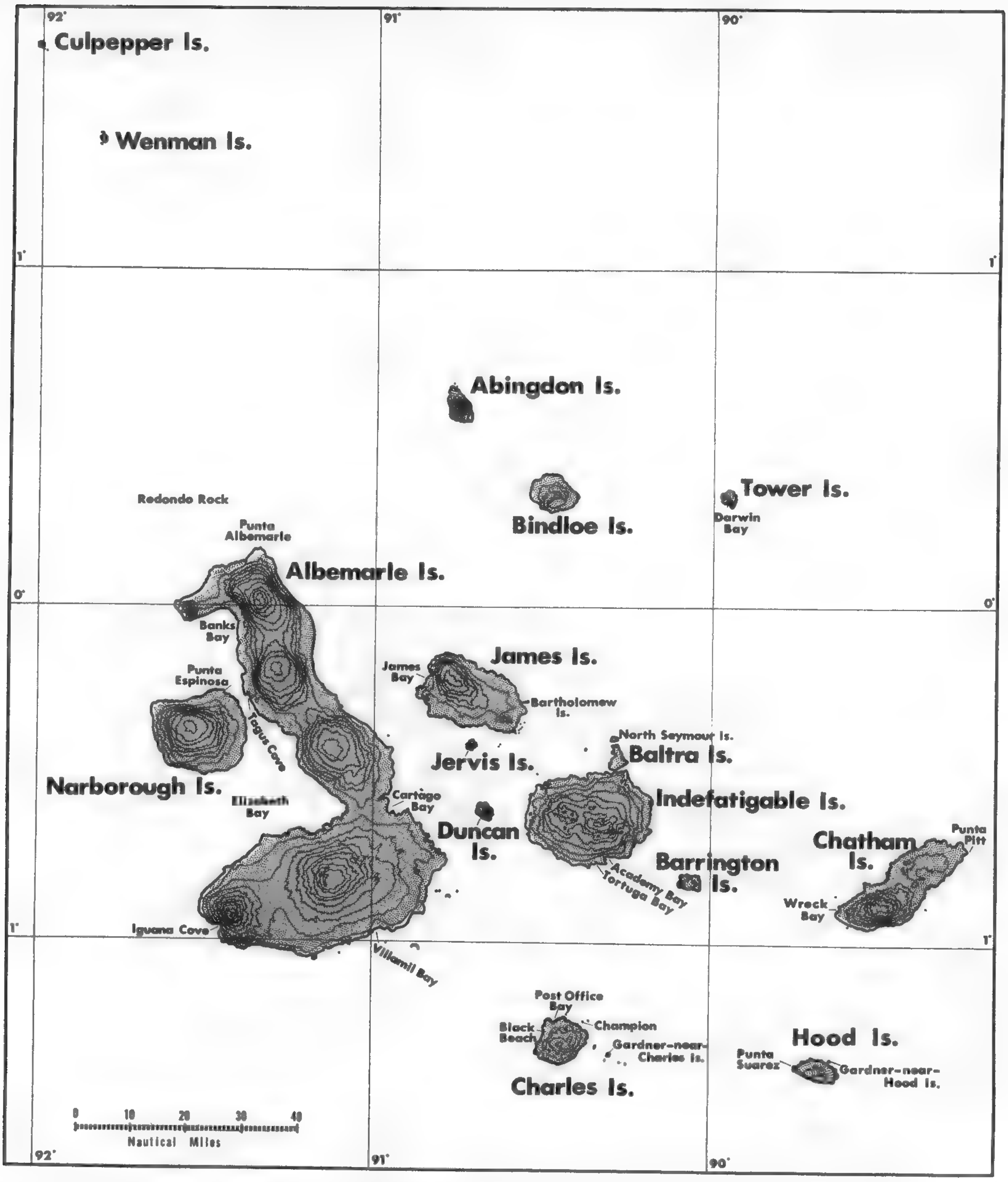

Figure 1. Map of the Galapagos Archipelago.

Occurrence of Egg-pecking Behavior in Galapagos Mockingbirds

One of the first behavioral traits of Galapagos mockingbirds noted by field-naturalists was the habit of attacking the eggs of other species of birds. Mr. Rollo H. Beck, museum collector and Galapagos explorer, described (*in* Rothschild and Hartert, 1902:383) two of his encounters with this behavior: After taking a finch nest on Abingdon Island, "... I tracked off to shoot the parent, and while so doing one of the mockers flew to the nest lying on the ground, picked one of the eggs, and but for my rapid interference, would undoubtedly have finished the other two. This action was similar to that of the mockers on Hood Island on our trip in 1897, when they tried, by rolling and picking, to break Albatross' eggs which we placed in a pile while collecting other eggs."

Later observers added many more species to the list of those whose eggs were the object of mockingbird predation (Table 3). Seabirds constitute the largest group of victimized species, including the Galapagos Petrel (*Oceanodroma tethys*), Waved Albatross (*Diomedea irrorata,* Figure 4), Blue-footed Booby (*Sula nebouxii,* Figures 3 and 5), Masked Booby (*Sula dactylatra*), Great Frigatebird (*Fregata minor*), Swallow-tailed Gull (*Larus furcatus,* Figure 7), and Sooty Tern (*Sterna fuscata*). We also have reports of mockingbirds attacking the eggs of the American Oystercatcher (*Haemantopus palliatus*), Galapagos Dove (*Nesopelia galapagoensis*), a Darwin's finch (*Platyspiza crassirostris*), and two indigenous species of iguanids, the lava lizard (*Tropidurus* sp.) and the marine iguana (*Amblyrhynchus cristatus*).

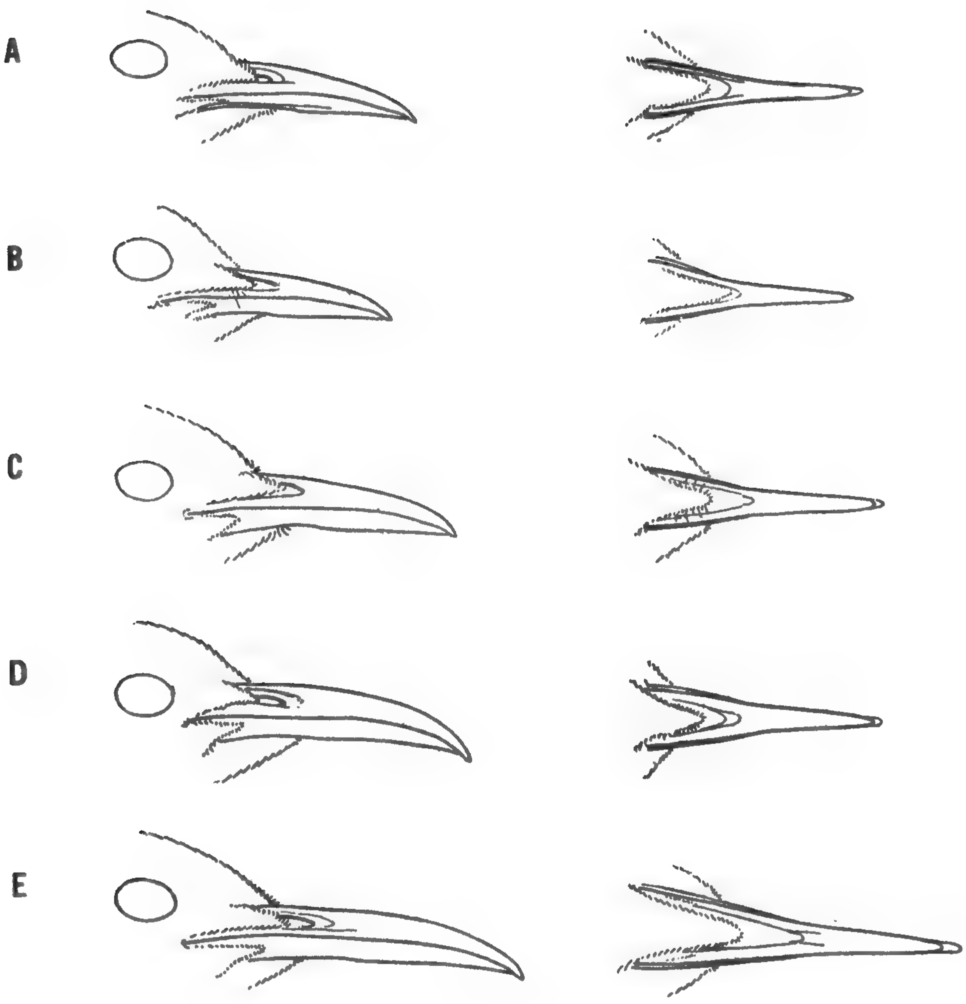

Figure 2. Bill profiles of male Galapagos mockingbirds. Lateral view on left, ventral view on right. A, *Nesomimus melanotis* (Chatham Island); B, *Nesomimus parvulus parvulus* (Albemarle Island); C, *Nesomimus parvulus bauri* (Tower Island); D, *Nesomimus trifasciatus* (Gardner-near-Charles Island); and E, *Nesomimus macdonaldi* (Hood Island). After Swarth, 1931, Figures 12 and 13.

In most instances, human intrusion of the nesting site precipitated egg-pecking by causing the adult bird to leave the eggs exposed to attack by ubiquitous mockingbirds (Figure 4). Non-human factors are involved in the case of lizards, some albatrosses, petrels, and doves (Harris, 1968:269). Unlike the thinner shells of smaller birds, the larger and thicker shells of seabird eggs are nearly invulnerable to the forceful blows of the mockingbird bill, except when the shell is pipped or otherwise fractured.

TABLE 1

Comparative Data on Distribution, Bill Length, and Environment for Island Populations of Galapagos Mockingbirds

Species population[a]	*Relative*[b] *length of bill*	*Island*	*Relative*[c] *size of island*	*Number of*[d] *vegetation zones*	*Relative*[e] *size of flora*
N. parvulus hulli	10	Culpepper*	3	1	1
wenmani	8	Wenman	2	1	2
personatus	11	Abingdon*	10	3	12
bindloei	9	Bindloe	11	1	6
bindloei	6	Jervis	4	1	5
bindloei	5	James	14	4	14
parvulus	4	Baltra	7	1	8
parvulus	3	Indefatigable	16	4	13
parvulus	2	Albemarle	17	4	17
parvulus	1	Narborough	15	4	10
parvulus[f]	—	Duncan	5	2	11
bauri	13	Tower*	6	1	4
barringtoni	12	Barrington	8	1	7
N. melanotis	7	Chatham	13	4	15
N. macdonaldi	15	Hood and Gardner-near-Hood*	9	1	9
N. trifasciatus	14	Champion and Gardner-near-Charles*	1	1	3[h]
	—	Charles[g]	12	3	16

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[a] Nomenclature according to Swarth, 1931.

[b] On a scale of 15, the larger the number, the larger the relative size of the bill; culmen measurements, males only; from Swarth (1931:113).

[c] On a scale of 17, the larger the number, the larger the relative size of the island; from Bowman (1961:12).

[d] Altitudinal vegetation zones: 1 = dry; 2 = dry + transition; 3 = dry + transition + moist; 4 = dry + transition + moist + grassy; from Bowman (1961:12).

[e] On a scale of 17, the larger the number, the larger the relative size of the flora; from Stewart (1911 and 1915).

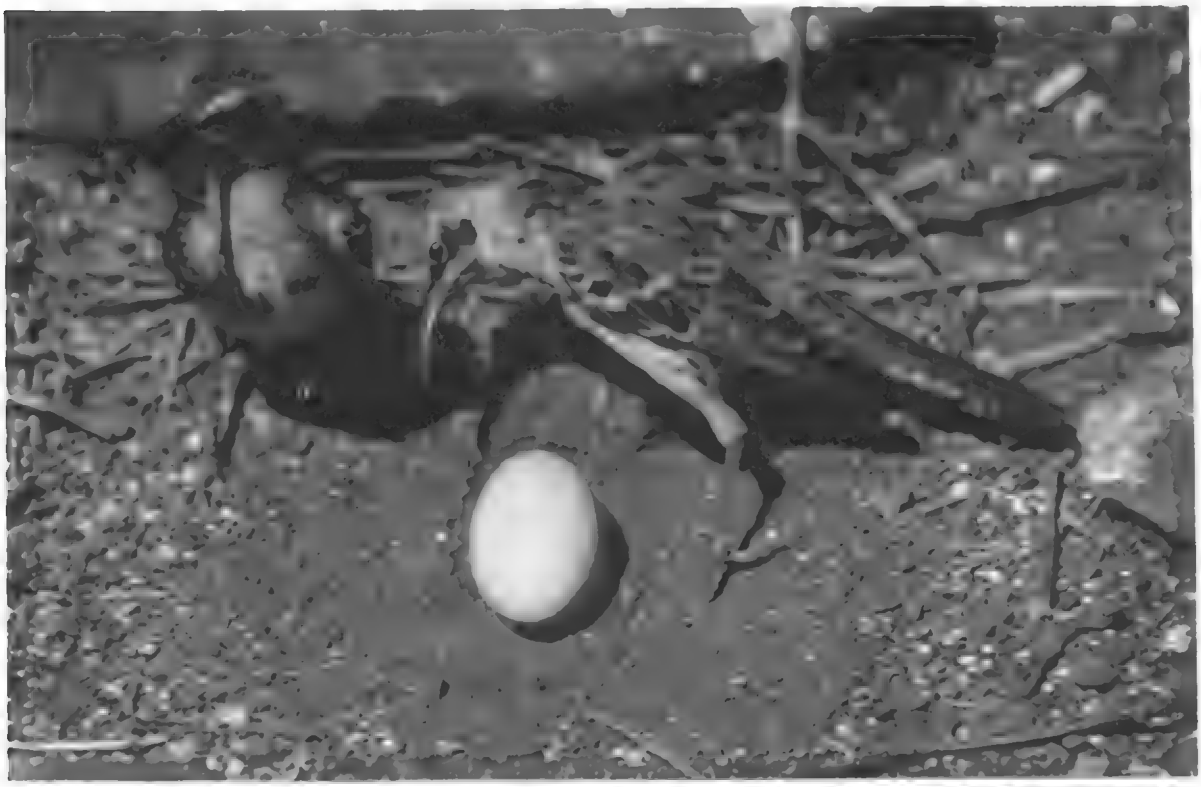
[f] Not resident on this island; see Gifford (1919:212).

[g] Presumed extinct, but see Swarth (1931:117).

[h] Estimate only: no precise floristic data are available for this island.

*Indicates that the mockingbird on this island is known to hunt for eggs. See Table 3.

The habit of pecking eggs and feeding on a wide variety of other animal and plant materials (Table 4) prompted Beebe (1924:78) to remark that the niche which the mockingbirds fill in the Galapagos includes those "... of all the brown thrashers, catbirds, wrens, creepers, bluebirds and thrushes of our northern fauna."



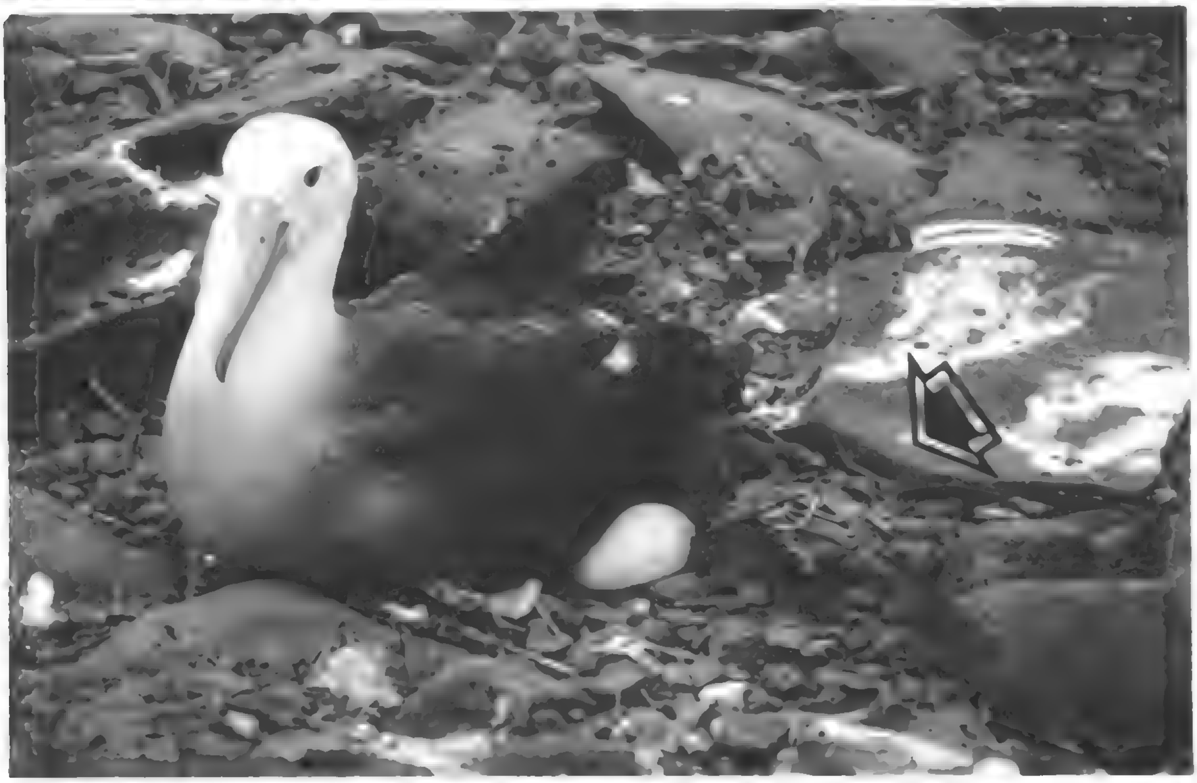


Figure 3 (*above*). *Nesomimus macdonaldi* on Hood Island. Pair investigating a Blue-footed Booby egg, which is about to be turned by sweeping the bill sideways beneath the egg.

Figure 4 *(below)*. A mockingbird, *Nesomimus macdonaldi* (indicated by arrow), on Hood Island, pecking at an egg of the Waved Albatross.

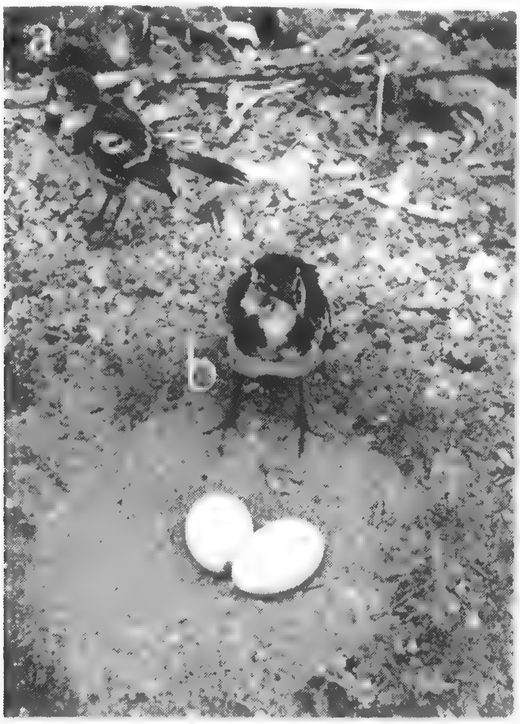
TABLE 2
Structural and Behavioral Differences between Island Populations of Galapagos Mockingbirds

Feature and authority	*Nesomimus trifasciatus (Gardner-near-Charles and Champion Islands)*	*Nesomimus macdonaldi (Gardner-near-Hood and Hood Islands)*	*Nesomimus melanotis (Chatham Island)*	*Nesomimus parvulus (Various islands)*
Plumage (Swarth, 1931)	Dark brown patches at sides of breast. See Figure 6	Least white spotting at end of rectrices	Practically no indication of a nuchal collar	Breast pure white, usually entirely unmarked
Bill length (Swarth, 1931); see Figure 2 and Table 1.	Slightly shorter than in *N. macdonaldi*	Longest	Medium length	Variable: small to long
Iris color (Rothschild and Hartert, 1899)	Seal-brown	Yellowish	Yellowish	Yellowish
Courtship posture (Venables, 1940)			Nape feathers not erected	Indefatigable Island, nape feathers erected
Feeding posture of fledged young (Gifford, 1919; Venables, 1940)		Tail elevated; wings raised and flapped; high screaming note	Tail drooped; wings drooped and quivered; bill agape with squeaking	Tower Island, tail and rear of body held higher than head; wings held slightly away from body
Song (Gulledge, 1970)	Greater percentage of AM frequencies; less stereotypy in syllable patterning	High percentage of FM syllables and source-generated harmonic spectra		High percentage of relatively pure non-frequency-modulated notes, with and without harmonic spectra
Water balance (Dunson, 1970)		Excessively thirsty: drinks 52–89 per cent of body weight per day		Indefatigable Island, drinks 14–30 per cent of body weight per day

Behavioral Differences between Island Species of Mockingbirds

Hatch (1965) originally claimed that only one species of Galapagos mockingbird, namely, *N. macdonaldi* on Hood Island, shows an interest in seabird eggs, and that "... this is an interesting example of a behavior pattern differing strikingly between closely related species."

Subsequently, Harris (1968) pointed out that, contrary to the opinion of Hatch, mockingbirds, *N. parvulus* on Tower Island and *N. trifasciatus* on Charles-near-Gardner Island, do, on occasion, display interest in the eggs of seabirds. In addition, he discovered that on Tower Island, as a result of competition between individuals of Galapagos Petrels for nest sites beneath slabs of lava, eggs are often ejected from the nests and later eaten by mockingbirds (compare with Nelson, 1966:430). In similar sites he found the broken eggs of Galapagos Doves, which he attributed to mockingbird attacks. Harris stated that "... at least two species of mockingbirds, and possibly three, regularly steal eggs, and that the fourth species [*N. melanotis* on Chatham Island] has little opportunity to do so." He concluded that the four species of Galapagos mockingbirds "... may well have different behavior patterns, but egg-stealing does not appear to be one of them."



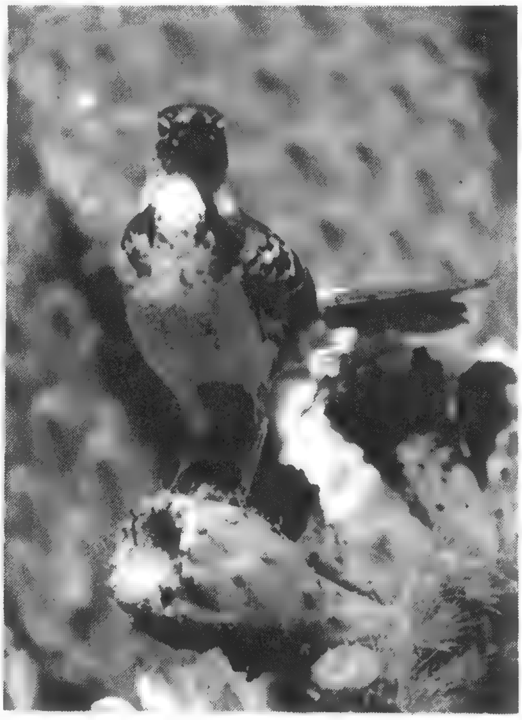


Figure 5 (*left*). *Nesomimus trifasciatus* on Gardner-near-Charles Island stopped initially at position (a) to examine the exposed eggs of a Blue-footed Booby, and then moved to position (b) without pecking the eggs (composite photograph).

Figure 6 (*right*). *Nesomimus trifasciatus* on Champion Island perched on *Opuntia* "pear" on which it feeds. Note conspicuous lateral breast patches, distinctive of this species.

Bowman confirmed the fact that *N. parvulus* on Tower Island and *N. trifasciatus* on Champion and Gardner-near-Charles Islands do, indeed, show an interest in seabird eggs (Table 3 and Figure 5). Although Hatch (1965) erred when he stated that the mockingbirds on these islands were indifferent to the seabirds among which they live, he correctly observed that the behavior pattern — i.e., pecking of the large seabird eggs — does differ between closely related species, albeit not "strikingly" as he claimed. As discussed below, the difference seems to be of a quantitative, rather than a qualitative, nature.

TABLE 3

Observations on Egg-hunting Habits of Galapagos Mockingbirds

Species victimized	*Island*	*Observations*	*Authority**
Seabirds	Hood	Rolled and pecked albatross eggs	Beck *in* Rothschild and Hartert, 1902:382
		Pecked through shell of albatross egg and devoured embryo (see Figure 4)	Gifford, 1919:208
		Examined unattended albatross egg without pecking shell	17 July 1967
		Turned abandoned albatross eggs over and over with bill	9 January 1962
		Attacked unattended albatross egg	Lévêque, 1964:35
		Gorged on albatross eggs that had been accidentally cracked	Peterson, 1967:581
		In December, pecked unattended eggs of Blue-footed and Masked Boobies; never broke undamaged eggs; opened only cracked ones	Hatch, 1965:355
		Frequently attacked unattended eggs of albatross, Blue-footed and Masked Boobies, and Swallow-tailed Gull	Harris, 1968:269
		Pecked through shell of unattended egg of Swallow-tailed Gull (see Figure 7)	16 October 1957
		About to peck eggs of unidentified species	Beebe, 1924: Figure 77
	Tower	Poised over unattended egg of Great Frigatebird	17 August 1957
		Pecked unguarded egg of Swallow-tailed Gull; shell undamaged	17 August 1957
		Fed on ejected eggs of Galapagos Petrel and unattended eggs of Great Frigatebird	Harris, 1968:269
	Champion	Evidence of pecking on deserted eggs of Blue-footed Booby	13 February 1967
	Gardner-near-Charles	Inspected, without pecking, two fresh eggs of Blue-footed Booby (see Figure 5)	19 July 1967
		Implicated in disappearance of nestling and hatching egg of Blue-footed Booby	Harris, 1968:269
	Culpepper	Fed on fresh egg of Sooty Tern; bill smeared with yolk	30 January 1964
Oystercatcher	Hood	Implicated in disappearance of two fresh eggs	7 January 1962
		Implicated in loss of two eggs in nest on 30 November 1961	Lévêque, 1964:34

TABLE 3 *(Continued)*

Species victimized	*Island*	*Observations*	*Authority**
Dove	Hood	Took eggs from under lava slabs	Harris, 1968:269
	Tower	Took eggs from under lava slabs	Harris, 1968:269
Finches	Abingdon	Pecked into eggs of *Platyspiza crassirostris* in nest	Beck *in* Rothschild and Hartert, 1902:382
	Tower	Entered newly completed nest of *Geospiza magnirostris* in which eggs had not been laid	6 February 1967
Chicken	Narborough	Attracted to scrambled eggs in open pan (see Figure 9)	15 July 1968
Lizards	Unspecified	Carried off egg of *Tropidurus* lizard	Hatch, 1965:355
		Fed on eggs of marine iguana	Hatch, 1965:355

*From field notes of R. I. Bowman, on file at the Vertebrate Museum, Division of Biology, San Francisco State College, when authority is not listed.

It is, perhaps, not surprising that mockingbirds show specific differences in their behavioral reactions to the eggs of other species, in view of the well-known differences in bill sizes (Swarth, 1931), and the environmental conditions on the various islands (Bowman, 1961). See Tables 1 and 7.

Marked inter-island variation in mockingbird behavior exists for courtship posture in adults and feeding posture of fledglings (Venables, 1940), water balance (Dunson, 1970), and song (Gulledge, 1970). See Table 2. Similarly, we know that other species of Galapagos vertebrates have distinct inter-island differences in behavior: food-getting in Darwin's finches (Bowman, 1961; Bowman and Billeb, 1965), their response to predators (Curio, 1964), and courtship bobbing in lava lizards (Carpenter, 1966).

Objective of Experiments

When we assembled several wild-caught mockingbirds in our San Francisco aviaries for vocalization studies, we had an opportunity to investigate, under controlled conditions, the egg-pecking behavior in three species, and to confirm field impressions of that behavior.

We designed the experiments so as to measure the amount of the differences in the species' reaction to a variety of egg-types, and to help explain the motivation and possible evolutionary significance of the behavior.

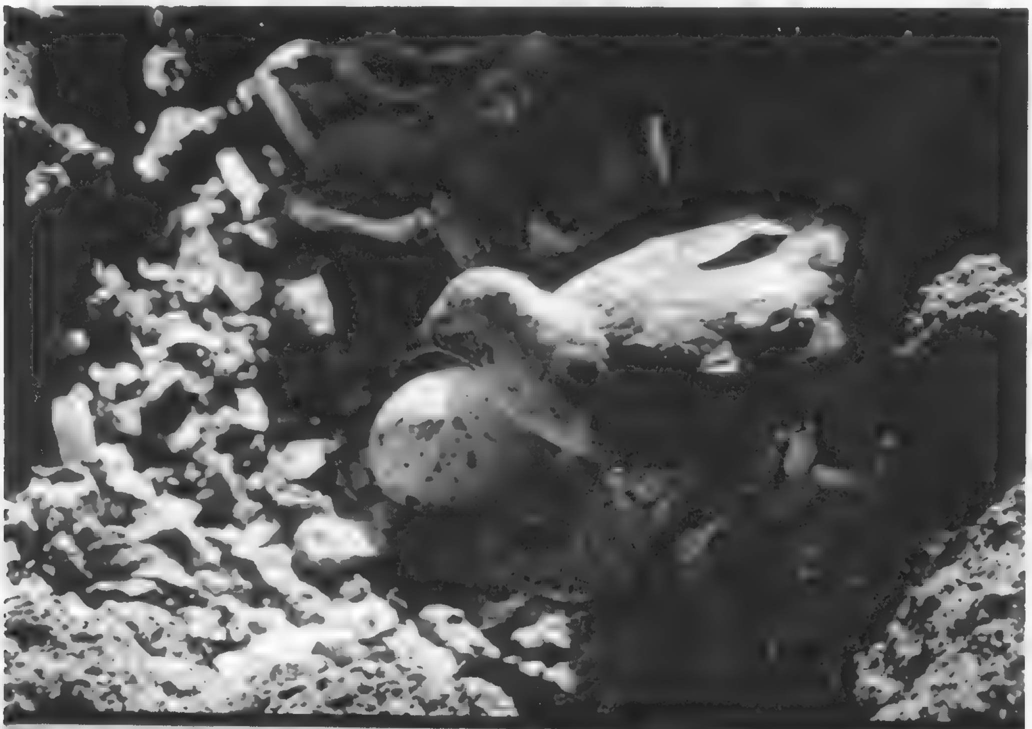
Materials and Methods

We placed members of three species of Galapagos mockingbirds in walk-in cages, approximately 4 × 8 × 10 feet, and segregated them in the following manner: Two adults of *N. macdonaldi* from Hood Island, referred to below as Bird A and Bird B, shared one cage. The only obvious difference between these two healthy birds was that Bird A had undergone amputation of the right foot at the lower end of the tarsus several years earlier. Bird A used the stump leg in more or less normal fashion in standing.

One adult *N. trifasciatus* from Champion Island, healthy and without physical defects, was caged alone.

One adult *N. parvulus parvulus* from Indefatigable Island was also caged alone. The bird's right foot showed some rigidity but we do not believe that this minor disability influenced its responses in any significant way. Foot disorders are fairly common in Galapagos mockingbirds in their natural environment (Gifford, 1919:212).

We offered the mockingbirds medium sized chicken eggs, colored and patterned to resemble the eggs of seabirds and iguanas that the birds might normally encounter in nature. We used six types consistently throughout the



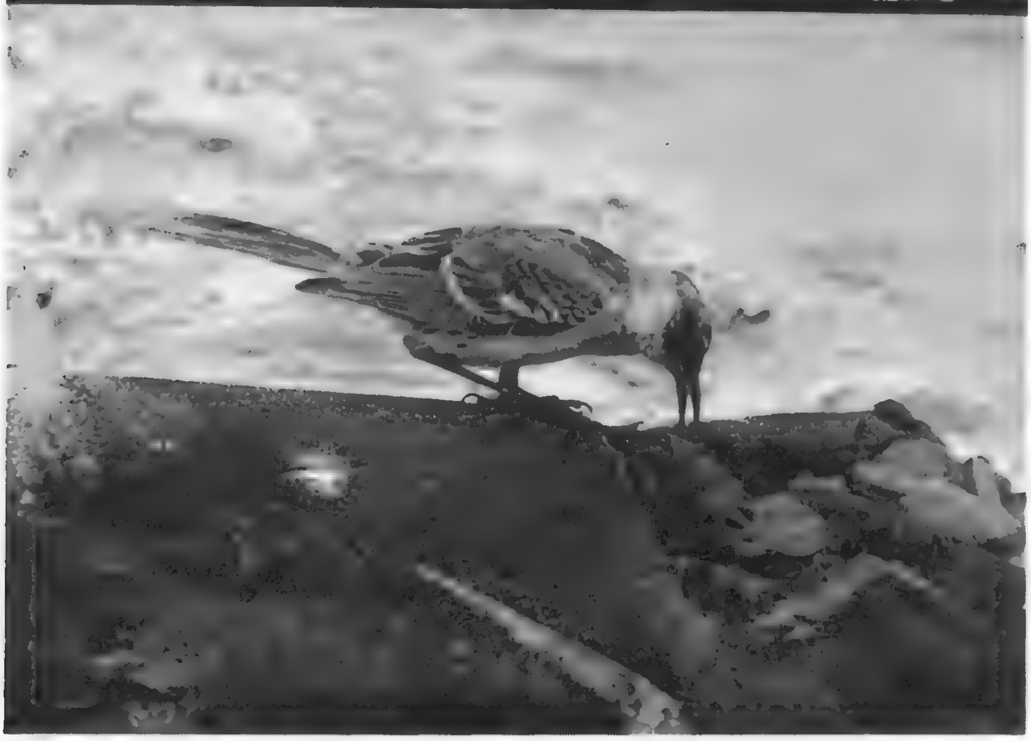


Figure 7 (*above*). *Nesomimus macdonaldi* on Hood Island investigating an exposed egg of a Swallow-tailed Gull.

Figure 8 (*below*). *Nesomimus parvulus* on Barrington Island feeding on a sea lion carcass.

experiments (Figure 12): Type A, plain white, to represent a Waved Albatross egg, which is about twice as large, or marine or land iguana eggs, which are somewhat smaller and oblong in shape; Type B, plain white with a red oval mark about three-fourths inch long, to resemble an egg, broken at some later state of embryonic development; Type C, plain white and marked with black "crack" lines, to test the observation that *N. macdonaldi* showed more interest in damaged eggs (Hatch, 1965); Type D, pale blue with numerous black spots, to simulate a wide range of variation in gull eggs, particularly those of the Swallow-tailed Gull (see Rothschild and Hartert, 1899:190; also see Nelson, 1968:30, who observed that black spots painted on shells "provoked intense attempts to get inside"); Type E, chalky blue, to resemble the egg of the Blue-footed Booby (see Figures 3 and 5), a common nesting species on many of the smaller islands (Table 7); Type F, a chicken-shaped, plastic toy egg of normal size, whose halves — one red and one yellow — snapped together, to represent an extreme in coloration that could not be duplicated in the natural environment.

The Nature of the Trials

During the course of the investigation, we conducted seven different trials (Table 5). In the first three trials we maintained normal feeding schedules and included all the experimental Galapagos mockingbirds. The fourth trial, conducted following a fasting period of 24 hours, also involved all the birds. In addition to the Galapagos mockingbirds described above, the first four trials included one Long-tailed Mockingbird (*Mimus longicaudatus punensis*) from southwestern Ecuador. This mainland mimid, housed in a separate cage with several Darwin's finches, showed behavior contrasting markedly with that of the Galapagos mockingbirds in that it steadfastly showed absolutely no response to the eggs placed in its cage, regardless of type, condition, or feeding schedule.

The fifth and sixth trials tested reactions of *N. trifasciatus* and *N. p. parvulus.* For the fifth trial, we placed fresh, unmarked, white, broken chicken eggs in the respective cages in the afternoon previous to the day of testing to encourage interest in eggs by permitting the birds to eat palatable egg protein and yolk. For the sixth trial, we placed plain, white, unbroken chicken eggs in the cages following a 24-hour fasting period, with the intention of measuring the bird's ability to break through the shell. The seventh and final trial, conducted 19 days after the sixth, measured the lasting effect of whatever learning had taken place. During the seventh trial, we presented a small rock to the birds to ascertain whether or not the pecking response was mere curiosity that any foreign object might elicit.

Our procedure during all seven trials was consistent, but we varied the order in which we presented the different eggs to the birds. As we placed an egg on the floor of the cage, we started a stopwatch in order to measure the seconds until a mockingbird directed the first peck at the egg. This period, referred to as the *response time,* was taken as a measure of the interest displayed by the bird — the shorter the response time, the greater the initial interest. Immediately after recording the response time, we started the stopwatch again to measure the interest span. We stopped the watch when the bird appeared to have lost interest in the egg, indicated by cessation of pecking and by wandering to other parts of the cage. This period, referred to as the *interest*

TABLE 4

General Feeding Habits of Galapagos Mockingbirds

Food	*Island*	*Observation*	*Authority**
Blood	Hood	Pecked at bleeding wounds on albatross feet	Root, *in* Harris, 1968:269
		Fed on coagulated blood of marine iguana on rock	7 January 1962
		Pecked at bloody cloaca of standing Blue-footed Booby	Nelson, 1968:30
Nestling seabird	Hood	Killed and ate newly hatched Masked Booby	Amadon, 1966:21
Lava lizard	Hood	Chased animal; pecked at cloaca of dead animal	23 September 1957
	Gardner-near-Hood	Fed on self-detached wiggling tail	21 September 1957
	Indefatigable	Pulled off tail	Beebe, 1924:71
		Killed lizard (see Figure 11)	12 December 1961
House mice	Indefatigable	Killed diurnal animals with bill in *Scalesia* forest**	9 August 1957
Feces	Narborough	Regularly inspected and pulled apart dried land iguana droppings	13 July 1968
	Indefatigable	Ate fresh green droppings of marine iguana	15 August 1968
	Hood	Ate soft droppings of seabirds	16 July 1967; Binford, 1971:25
		Ate sea lion droppings	Nelson, 1968:30
Dead vertebrates	Hood	Pecked at eyelid of dead Brown Pelican	Gifford, 1919:208
		Fed on carcass of frigatebird	16 October 1957
		Pecked at molting scales of marine iguana	17 July 1967
		Fed on jerked goat meat	Nelson, 1968:30
		Fed on sea lion carcass	16 October 1957; 6 January 1962
	Barrington	Fed on flesh of slaughtered sea lion (see Figure 8)	12 December 1961
	Narborough	Ate entrails of land iguana	9 September 1957
Terrestrial arthropods	Narborough	Removed ticks from land iguana which assumed cooperative position	15 July 1968
		Excavated ants and their eggs beneath bush	14 July 1968
	Culpepper	Attacked and killed centipede	30 January 1964
	Indefatigable	Ate freshly killed centipede	27 July 1967
		Pursued dragonflies in flight	Beebe, 1924:292
		Pursued carpenter bees in flight	12 December 1961
		Pursued grasshopper in flight	23 November 1961
	Champion	Pursued grasshopper in flight	18 January 1962
	Barrington	Pursued grasshopper in flight	20 December 1961
		Pursued flies in intertidal zone	17 December 1961

TABLE 4 *(Continued)*

Food	*Island*	*Observation*	*Authority**
	Tower	Ate cockroaches and geometrid larvae	11 and 18 February 1962
	Jervis	Ate dermestid beetle larvae from skeleton	30 July 1957
	Hood	Dug ant lions from funnel pits in soil	16 July 1967
Land snails	Indefatigable	Extracted soft parts by pounding snail against rock; left small heaps of broken shells beside stone anvil	30 November 1952
Marine invertebrates	Barrington	Ate nereid worms in intertidal zone	17 December 1961
	Tower	Pulled off leg of *Grapsus* crab	4 February 1961
Other animal food	Hood	Fed on oily regurgitated stomach contents of albatross	Nelson, 1968:155
Plants	Indefatigable	Ate *Opuntia* flowers, fruit, and pulp	8 November 1961
		Ate seeds of introduced trailside species of gourds (Cucurbitaceae)	18 February 1953
		Ate *Parkinsonia* flowers	23 July 1967
	Tower	Ate *Opuntia* flowers	20 February 1962
		Ate *Cordia* fruits	18 August 1957
	Hood	Ate *Opuntia* fruits	21 September 1957
	Wenman	Ate *Opuntia* fruits and flowers	21 January 1964
	Barrington	Ate *Opuntia* fruits and flowers	18 December 1961
	Champion	Ate *Opuntia* fruits and flowers (see Figure 6)	19 January 1962; 16 February 1967
	Gardner-near-Charles	Ate *Convolvulus* flowers	19 July 1967

*From field notes of R. I. Bowman, on file at the Vertebrate Museum, Division of Biology, San Francisco State College, when authority is not listed.

***N. macdonaldi* from Hood Island effectively route and kill mice in outdoor aviaries in San Francisco.

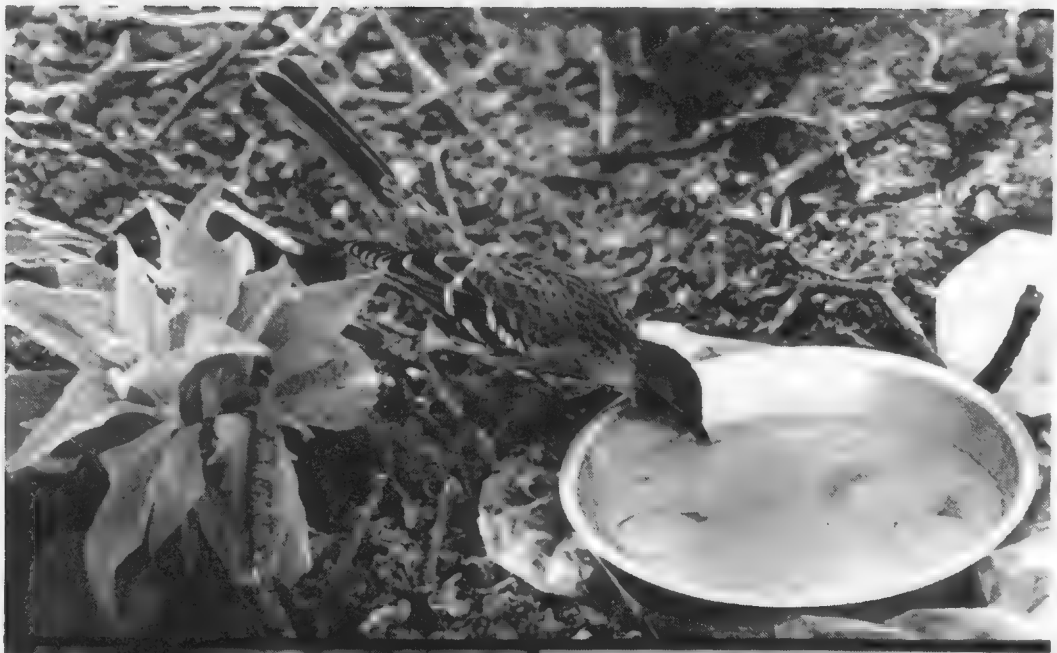
span, we interpreted as an indication of the extent to which the bird's interest had been aroused, and as a gauge of the susceptibility of the bird to further learning. The *number of pecks* that we counted served as a useful index of the egg-pecking activity of the bird.

We repeated the foregoing procedure with each egg-type for every trial, except for Trial 4, when we inadvertently omitted Egg-type D from the test series presented to *N. trifasciatus,* and Egg-type E from the test series presented to *N. p. parvulus.*

Results and Discussion

Nesomimus macdonaldi from Hood Island

Throughout the five trials involving this species, Birds A and B always showed interest in eggs placed on the floor of their cage (see Tables 5 and 6). In spite of its physical disability, Bird A, which we presumed to be a male, always took possession of the eggs as soon as we placed them in the cage. Both birds responded immediately and flew down to inspect the eggs; but Bird A



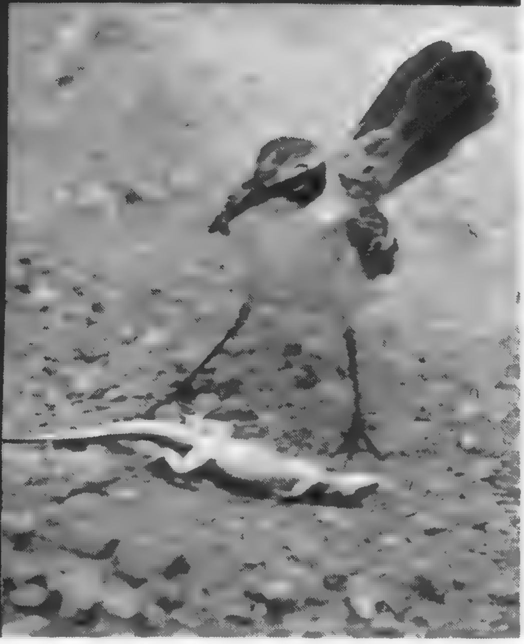


Figure 9 (*above*). *Nesomimus parvulus* on Narborough Island feeding on broken chicken eggs prepared for cooking.

Figure 10 (*below left*). Culpepper Island bird killing a centipede.

Figure 11 (*below right*). *Nesomimus parvulus* on Indefatigable Island preparing to feed on a lava lizard (*Tropidurus* sp.).

usually directed a warning call, accompanied by one or two short aggressive runs, at Bird B, which we presumed to be a female. With Bird B away from the immediate area of the egg, Bird A then began to peck the egg and tried to roll it over with side-swipes of the bill. After varying periods of time, Bird A lost interest in the egg and wandered off. Often, as Bird A lost interest, Bird B approached the egg and began pecking it. This activity always brought Bird A back to reclaim the egg and chase Bird B off again. The two birds repeated this behavior with each trial throughout the study, and since the reactions of Bird B were invariably thwarted by Bird A, the data presented for *N. macdonaldi* relate only to Bird A.

Under normal feeding conditions, *N. macdonaldi* responded to all seven egg-types (Figure 13) but with considerable variation in response time and interest span. Egg-type F, the red and yellow, rated as first choice with the shortest response time and the longest interest span. This egg-type consistently rated high with all three species of mockingbirds (see Figures 13 and 14). Since this bright two-colored egg was not intended to simulate any natural egg in the Galapagos environment, we find it difficult to explain the birds' attraction to it. The birds displayed a preference for the yellow end of the egg by directing all their pecks at this area. At one time during the trials, Bird A pecked so feverishly at the red and yellow plastic egg that the two halves separated, causing a great flutter. Both birds then proceeded to peck at the inside of the two upturned cups.

Tinbergen (1961) demonstrated that many gulls peck more often at red objects in the nest than at objects of other colors. Studies by Schwartzkopf (1960) showed that the eyes of all species of birds examined — Galapagos mockingbirds not investigated — are sensitive to the same spectral range as human beings. The indications of a slightly reduced sensitivity to blue in diurnal birds may explain, in part, the relatively low level of response to Egg-type E — plain chalky blue — by both *N. macdonaldi* and *N. trifasciatus,* despite the fact that this egg resembled Blue-footed Booby eggs which, in the wild, attract both species (see Figures 3 and 5).

Except for the red and yellow Egg-type F, Egg-types A, B, and C — all essentially white — were the most stimulating to *N. macdonaldi* under normal feeding conditions, and to *N. trifasciatus* and *N. p. parvulus* following a period of fasting.

Tests made by Tinbergen *et al.* (1962), using eggshell dummies in which color, shape, size, and distance from the nest were varied, showed that nesting Black-headed Gulls pick up and carry objects of all colors, but that khaki, the normal ground color of the egg, and white are particularly stimulating and that green elicits very few responses.

Under conditions of fasting (Figure 13), *N. macdonaldi* failed to respond to the "cracked" egg (type C) although, in most cases, its response time to the other egg-types was reduced and the interest span lengthened. Working with hungry birds in the field, Hatch (1965) found that a spidery asterisk pencilled on the egg of a Waved Albatross specifically attracted the pecks of *N. macdonaldi.*

Egg-type D, designed to resemble the eggs of the Swallow-tailed Gull, proved comparatively ineffective in evoking an egg-pecking reaction despite the observation of Nelson (1968:30) that black spots painted on the shell provoked a vigorous response in the wild.

Under the normal feeding regime, we recorded the greatest pecking intensity (Figure 14) in *N. macdonaldi* for Egg-type F, the red and yellow, and somewhat less for Egg-type B, red spot on white. Following a 24-hour fasting period, the number of pecks at Egg-types A, plain white, and F, red and yellow, increased one hundred fold, while at the same time the interest span doubled for Egg-type A and decreased slightly for Egg-type F (Figure 13). When we compare the average data on all egg-types for Trials 3 and 4 (Table 6), it is clear that, after a 24-hour fast, the response time is halved, the interest span is lengthened by about 30 per cent, and the incidence of pecking is almost doubled.

During Trial 7, both *N. macdonaldi* birds eyed the introduced rock from a distance, slowly approached and circled it, and then wandered off. They did not rush up to the rock as they did to eggs placed in the cage, nor did they peck at it or attempt to roll it over.

Finally, Birds A and B showed very little fear and a great deal of curiosity at the presence of the experimenter in the cage. As we entered the aviary, the birds ran to the front of the cage and, for as long as we remained within sight, watched intently. Most observers in the field have remarked about the extreme tameness of the mockingbirds on Hood Island and their inordinate curiosity (see Nelson, 1968:6, photo 4). In the wild, *N. macdonaldi* sometimes investigates so closely that an observer may capture the bird by hand (Peterson, 1967:570).

TABLE 5

Resumé of Trials and Results of Egg-pecking Experiments with Galapagos Mockingbirds*

Trial number	*Date*	*Species tested*	*Feeding conditions*	*Variations in experiment*	*General results*
1	22 March	4	normal	none	*N. macdonaldi:* active response *N. trifasciatus:* no response *N. p. parvulus:* no response *M. longicaudatus:* no response
2	2 April	4	normal	none	*N. macdonaldi:* active response *N. trifasciatus:* agitated by eggs *N. p. parvulus:* slight interest *M. longicaudatus:* no response
3	3 April	4	normal	Broken egg left overnight with *trifasciatus* and *parvulus*	*N. macdonaldi:* active response *N. trifasciatus:* broken egg untouched; response only to red/yellow egg *N. p. parvulus:* broken egg half eaten; some interest *M. longicaudatus:* no response
4	5 April	4	24-hour fast	none	*N. macdonaldi:* active response *N. trifasciatus:* active response** *N. p. parvulus:* selective response to eggs offered*** *M. longicaudatus:* no response
5	6 April	2	normal	Broken egg left overnight	*N. trifasciatus:* broken egg all eaten; response to other eggs slightly reduced *N. p. parvulus:* broken egg one-third eaten; response to other eggs reduced
6	7 April	2	24-hour fast	Unbroken egg left overnight	Unbroken eggs intact. Immediate response to fresh broken eggs
7	26 April	3	normal	Small rock offered	*N. macdonaldi:* active response *N. trifasciatus:* slight reaction to red/yellow egg *N. p. parvulus:* no response All species: no response to rock

*Additional information in text, in Table 6, and in Figures 12, 13, and 14.

**Egg-type D omitted from test.

***Egg-type E omitted from test.

Nesomimus trifasciatus from Champion Island

This species showed quite a different response to the investigator and the eggs, being generally more fearful than *N. macdonaldi* and appearing cautious of all objects within its view. Thus, while performing the trials, the investigator had to step out of sight of the bird and observe it through the semi-transparent, plastic walls of the cage.

During the first two trials, the response exhibited by *N. trifasciatus* changed from merely "eyeing" the egg from its perch to hopping excitedly from perch to ground and back and running back and forth past the egg on the cage floor. Preceding the third trial (Table 5), we left a broken egg overnight in the cage. It appeared to have been untouched when we removed it the following morning. The bird's interest in eggs continued to grow until, during the third trial, it stopped and pecked twice at Egg-type F, red and yellow, having failed to peck at all other egg-types offered during the trial. Following 24 hours of fasting, this bird pecked at all egg-types offered (Figure 13), but still clearly preferred the red and yellow egg. However, Egg-type A, the plain white egg, was next in line of preference as measured by the number of pecks (Figure 14).

Preceding the fifth trial, we again left a broken egg overnight in the cage. The following morning the egg had been completely devoured, with the shell broken up and scattered about the floor. During Trials 5 and 6, *N. trifasciatus* responded well to many egg-types (see Table 6); but 19 days after Trial 6, the bird responded only to Egg-type F, reminiscent of its initial choice in Trial 3. It completely ignored the stone in Trial 7.

Nesomimus p. parvulus from Indefatigable Island

This bird showed less activity than the other two species tested. The somewhat rigid condition of the right foot at times may partially explain some of its subdued behavior. Occasionally, the bird's preoccupation with pecking at the foot made it difficult to gain the bird's attention. During the first two trials, conducted under a normal feeding regime, this mockingbird showed very little reaction to the eggs placed on the floor of the cage. However, preceding the third trial, a broken egg left on the floor was almost half eaten by the following morning.

During the third trial the bird reacted more strongly than previously by squawking almost continuously when we put the test eggs in the cage, but still refused to fly down to inspect them. Following 24 hours of fasting for Trial 4 (Table 5), the bird responded to Egg-types A, B, and F (see Figure 13). The mockingbird responded similarly during Trial 5, but we obtained no response to the eggs during Trials 6 and 7 or to the rock in Trial 7.

Role of Learning in Egg-pecking Behavior

These experiments seem to demonstrate the ways in which motivational factors affect behavior. The internal stimulus, hunger, increased the activity — the search behavior — in all three species of mockingbirds (Table 5, Trial 4), but especially in *N. trifasciatus* and *N. p. parvulus*. By presenting a variety of external stimuli in the six egg types, *N. macdonaldi* noticeably increased its food selectivity.

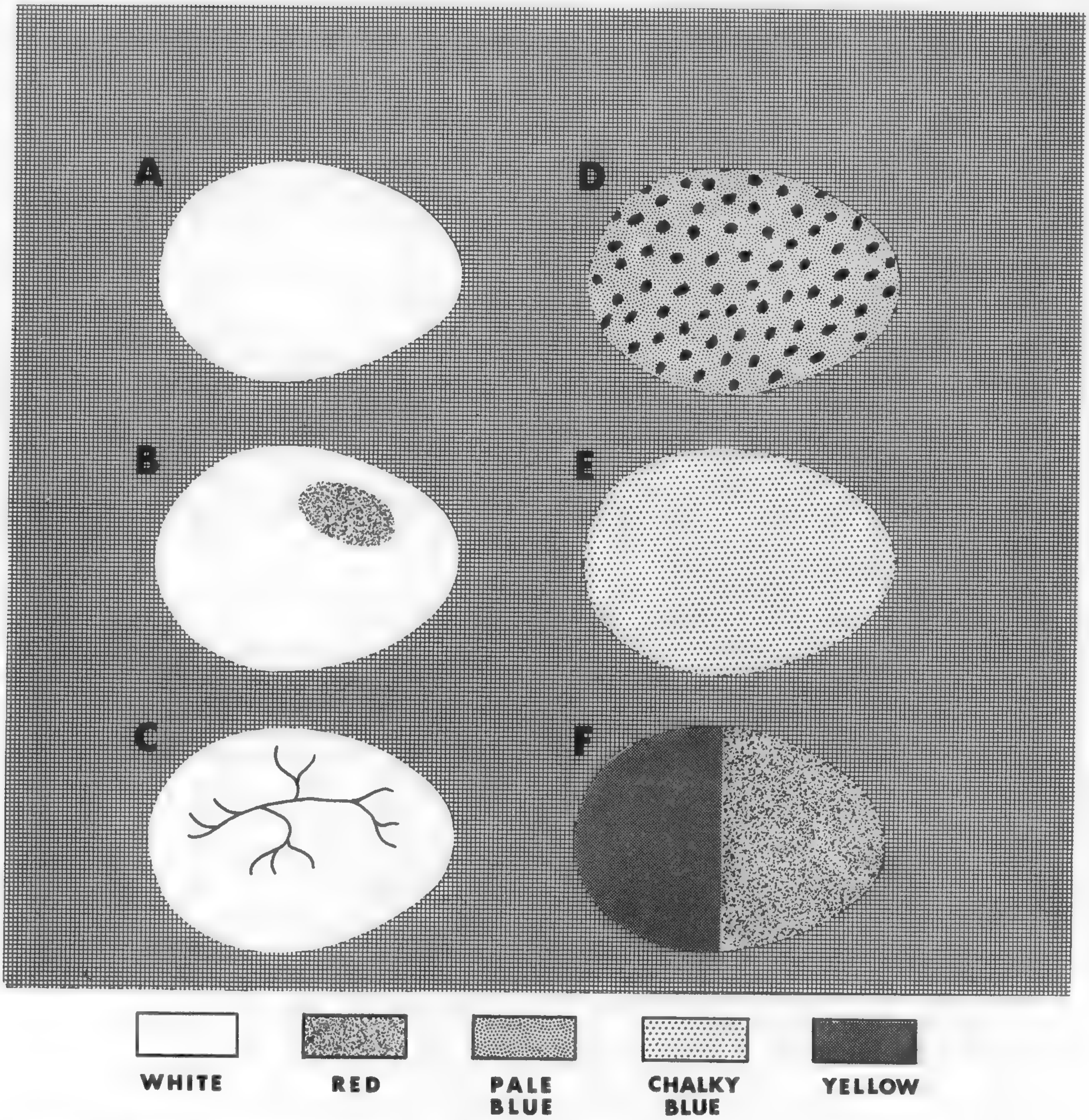


Figure 12. Shell patterns of chicken eggs used in pecking experiments. A, plain white; B, plain white with one red oval mark; C, plain white with black "crack" lines; D, black spots on pale blue ground-color; E, plain chalky blue; and F, plain yellow on blunt half and plain red on pointed half.

Whether or not food deprivation brought about an increase in activity by lowering the threshold of responsiveness to the environmental change (see Campbell and Sheffield, 1953), we cannot ascertain by these experiments. The results strongly support the guess made by Hatch (1965) that learning plays a significant role in the development of egg-pecking. But, contrary to Hatch's view — that other individuals of the same species are the source of the learning stimuli, a situation probably occurring in nature — the present study suggests that the particular internal condition, such as hunger, imposed on the bird may be just as important in motivating learning. *N. trifasciatus* and *N. p. parvulus* were caged alone and had no opportunity to observe the behavior in other birds. The frequent exposure of the mockingbirds to eggs seemed to induce interest and, after a brief period of time, to heighten curiosity. This contrasted directly with the complete lack of interest displayed by these same birds at the onset of the trials (Table 6). Overnight exposure to broken eggs seemed to intensify the response, but whether this occurred by "contiguity" or "reinforcement" learning cannot, of course, be determined from these experiments (see Hinde, 1966:414). The fact that between Trials 6 and 7, and without reinforcement of any kind, the most behaviorally recalcitrant species, *N. p. parvulus,* had regressed to approximately the same stage of responsiveness that prevailed in Trial 1, almost one month earlier, suggests that short-term learning was involved.

Behavioral Differences Related to the Environment

Field studies in the Galapagos indicate that the pecking of seabird eggs is clearly a behavioral peculiarity most prevalent among the mockingbirds of Hood Island (*N. macdonaldi*) and somewhat less prevalent among the populations on Tower, Champion, Gardner-near-Charles, and Culpepper Islands. We know little about this behavior on other islands. The race on Indefatigable Island (*N. p. parvulus*), which was used in the experiments, is not known to attack seabird eggs in the wild, and in this respect, as well as in bill size (Figure 2), it differs markedly from the race on Tower Island (Table 1), *N. p. bauri,* that has the longest bill of all races of the species (Swarth, 1931:113).

An analysis of the environmental conditions on the various islands of the Galapagos Archipelago (Table 1) indicates that the mockingbirds with egg-

TABLE 6

Averaged Data for Egg-pecking Experiments on Three Species of Galapagos Mockingbirds

*Trial**	*Nesomimus macdonaldi*			*Nesomimus trifasciatus*			*Nesomimus p. parvulus*		
	*Response time in seconds***	*Interest span in seconds*	*Number of pecks*	*Response time in seconds*	*Interest span in seconds*	*Number of pecks*	*Response time in seconds*	*Interest span in seconds*	*Number of pecks*
1	4	80	8	NR†	NR	NR	NR	NR	NR
2	17	64	13	NR	NR	NR	NR	NR	NR
3	4	67	12	35	20	2	NR	NR	NR
4	2	98	21	26	139	12	80	75	12
5	—‡	—	—	30	55	8	72	45	8
6	—	—	—	50	86	3	NR	NR	NR
7	4	50	12	19	45	4	NR	NR	NR

*Resumé of trials in Table 5.

**Average for all 6 egg-types (see Figure 13).

†NR = no response.

‡Species not tested.

pecking propensities are those which (1) have relatively longer bills, (2) live on the smaller, low-lying, more arid islands, (3) where seabirds nest in great abundance (Table 7), and (4) where the flora is relatively more depauperate.

The proportion of the mockingbirds' diet, made up of seabird eggs, might be expected to depend on the probability of the birds encountering such eggs while searching for food. Hunger may profoundly affect the birds by encouraging the adoption of a specific "search image." If mockingbirds seldom encounter eggs of other birds, as is true on most of the larger islands such as Indefatigable, Albemarle, Narborough, James, etc., then we could not expect the egg-pecking behavior to be maintained at a low threshold response-level. The fact that none of the three species of mockingbirds reacted to the small rock presented to them at the conclusion of the trials may indicate that they had developed a relatively strong "search image" for eggs.

By contrast, the mockingbirds *N. macdonaldi* on Hood Island frequently encounter fresh seabird eggs, which are available throughout most of the year. Additionally, a large number of abandoned eggs of the Waved Albatross lie scattered about the island. These large eggs endure intact for years, or until mockingbirds break them open or they decay gradually. Mass abandonment of eggs by seabirds occurs at irregular intervals when heavy tropical downpours, El Niño phenomenon, create pools in which successive generations of

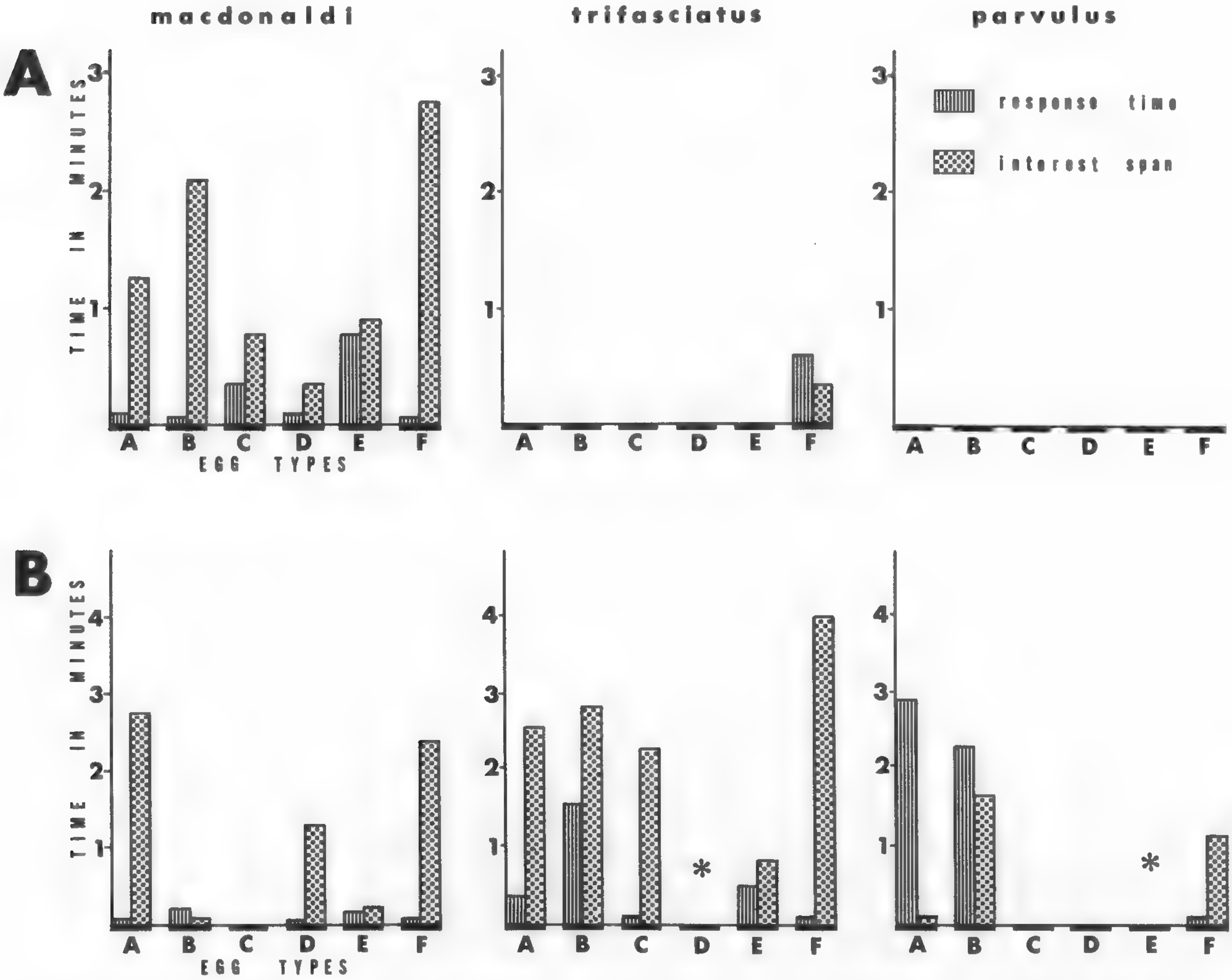


Figure 13. Response time in striped bars and interest span in stippled bars of three species of Galapagos mockingbirds to six color patterns of eggs. A, on a normal feeding regime, and B, after a 24-hour fasting. Asterisk indicates egg-type omitted from test. When comparing graphs A and B, note the more expanded time scale in A.

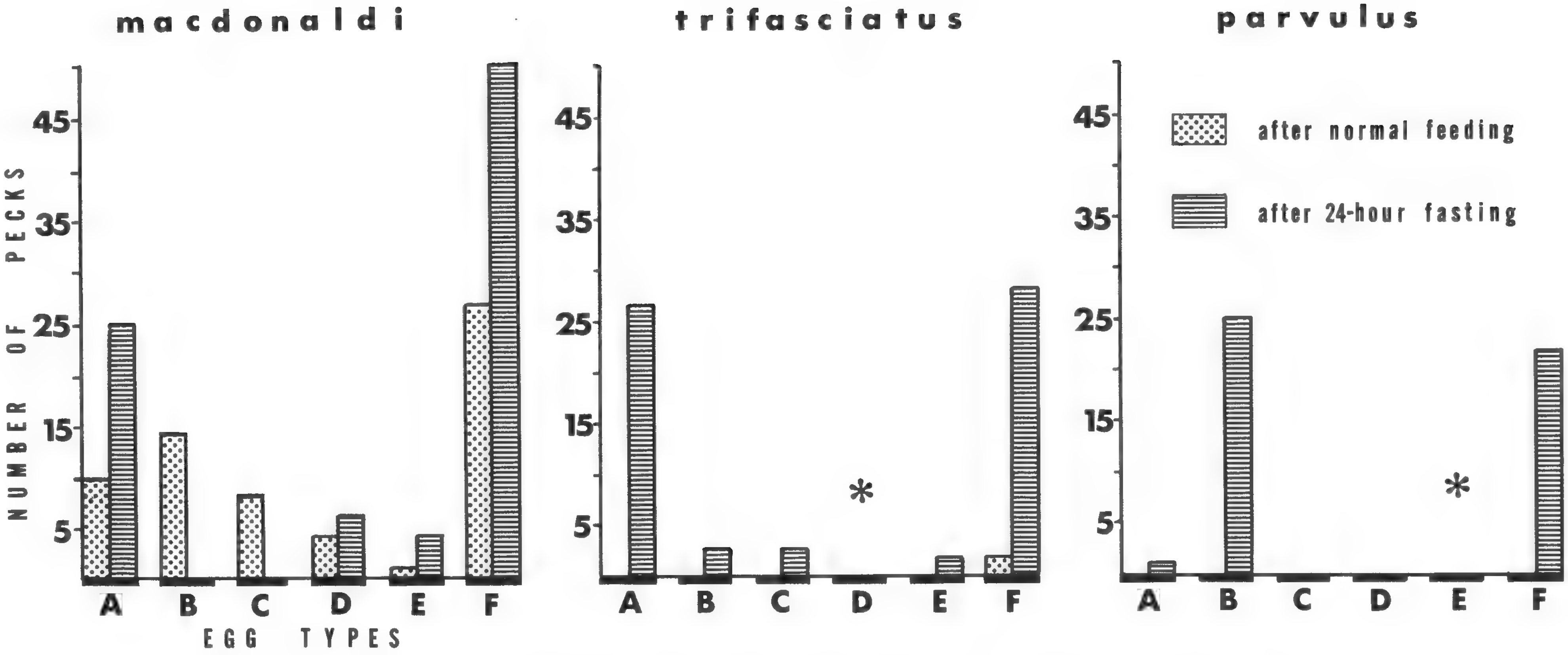


Figure 14. Pecking frequency of three species of Galapagos mockingbirds for six color patterns of eggs. Response under normal feeding schedule, stippled bars, and after 24-hour fasting, striped bars. Compare with Figure 13. Asterisk (*) indicates egg type omitted from test.

mosquitoes spawn and torment the incubating birds, ultimately driving them to sea (see Peterson, 1967:581–585).

Except for the abnormally wet conditions mentioned above, the nesting season of the albatross, from June to December, coincides with the driest time of year on Hood Island when surface food is scarce. In response to this stress, all resident land birds, including three species of Darwin's finches, a mockingbird, the Yellow Warbler (*Dendroica petechia*), a tyrant flycatcher (*Myiarchus magnirostris*), and the Galapagos dove turn to foraging at ground level where they dig in the shallow soil with feet and bill, turn stones, or disappear from view beneath loose slabs of lava. The region between the tides attracts all species of land birds regularly. Mockingbirds in immature plumage, captured by hand on 18 July 1967, had small, concave breast muscles, and birds in adult plumage showed no evidence of subcutaneous fat. As many as 30 mockingbirds pursued cast-off morsels of food at one time. It is not surprising, therefore, that mockingbirds should readily attack seabird eggs.

Tower Island harbors the world's largest nesting population of Red-footed Boobies (*Sula sula*), about 140,000 pairs, averaging about 90 pairs per 10,000 square yards (Nelson, 1968:43). Also on Tower Island, there is an extremely large nesting colony of the Galapagos Petrel on whose abandoned eggs the mockingbirds feed (Harris, 1968).

Although the population of mockingbirds on Champion and Gardner-near-Charles Islands probably numbers no more than 150 individuals (Harris, 1968), these islands are small; and nesting Blue-footed Boobies, Red-footed Boobies, and Swallow-tailed Gulls, offer mockingbirds year-round opportunity to encounter seabird eggs.

Significance of Bill Size

The long bills of many of the Galapagos mockingbirds resemble, to a greater degree, the North American thrashers (*Toxostoma* spp.) than the continental mockingbirds (*Mimus* spp.). In the Galapagos, the egg-eating species have distinctively longer and more robust bills than those birds which are not known to prey on eggs (Table 1). The primary adaptation of the long bill is for digging in the ground, and field observations indicate that the most powerful diggers have the longest and most curved bills. Engels (1940:350) noted a similar correlation of structure and function in thrashers. Presumably, on small Galapagos islands with their more restricted food resources, the evolutionary strategy for successful living involved the broadening of the food niche through exploitation of the more concealed foods. To reach these hidden sources selection favored the development of a longer, more curved bill. This structural feature, in combination with an insatiable curiosity, makes it possible for the mockingbirds to thrive in the rugged environment of the Galapagos, where a seasonal scarcity of foods is the rule. The marked tendency to peck at any strange object, and the suitability of the longer bills for reaching into holes and crevices in rocks, soil, and vegetation, probably led to probing at "cracks" in a hatching egg, at "holes" such as the cloaca of birds and iguanas, or the eyelets of a boot (see Figures 15 and 16; Tables 3 and 4).

The noteworthy characteristics of many island endemics involve their opportunism in food-getting. Darwin's finches of the Galapagos are singularly famous for their bizarre feeding habits that include tool-using (Millikan and Bowman, 1967), blood-eating (Bowman and Billeb, 1965), tick-grooming of marine iguanas (Amadon, 1966 and 1967), stone-turning (DeBenedictis, 1966), and even egg-pecking. David Cavagnaro (pers. commun.) saw an example of the egg-pecking behavior on 30 January 1964 atop Culpepper Island where he watched the relatively elongate-billed finch (*Geospiza difficilis nigrescens*) peck out a "window" in the shell of an egg of the Swallow-tailed Gull. And Bowman saw the same species, race *septentrionalis,* on nearby Wenman Island roll and peck the eggs of the Masked Booby in late January 1967; (see Harris, 1968).

In other regions of the Pacific, such as Laysan Island, Amadon (1966:21) reported that the Laysan Finch (*Psittirostra cantans*) and the Laysan Island Rail (*Porzanula palmeri*) eat the eggs of the local seabirds. In February 1968, on Isla Plata, 27 kilometers off the Ecuadorian coast at 1° 16′ S Lat., James Gulledge and Bowman saw the Turkey Vulture (*Cathartes aura*) breaking the

TABLE 7

Major Breeding Colonies of Seabirds in the Galapagos Islands

	Islands					
Species	*Hood*	*Tower*	*Wenman*[a]	*Culpepper*[b]	*Daphne Major*	*Champion and Gardner-near-Charles*
Waved Albatross	2,000 pairs[c]	—	—	—	—	—
Blue-footed Booby	500+ pairs[d]				Very large 400+ pairs[e]	X
Red-footed Booby		140,000 pairs[d]	Very large	Very large	—	X
Masked Booby	1,000 pairs[d]	5,000 pairs[d]	X	Large	X	X
Magnificent Frigatebird	—	X	—	—	—	X
Great Frigatebird	X[f]	hundreds[c]	X	X	—	—
Swallow-tailed Gull	Several thousand pairs[c]	1,000+ pairs[c]	Very large[c]	Moderately large	5,000+ pairs	X
Sooty Tern	—	—	—	5,000+ pairs	—	—
Red-billed Tropicbird	X	X	X	X	X	X

[a] R. I. Bowman, field observations, February 1964; April 1968.

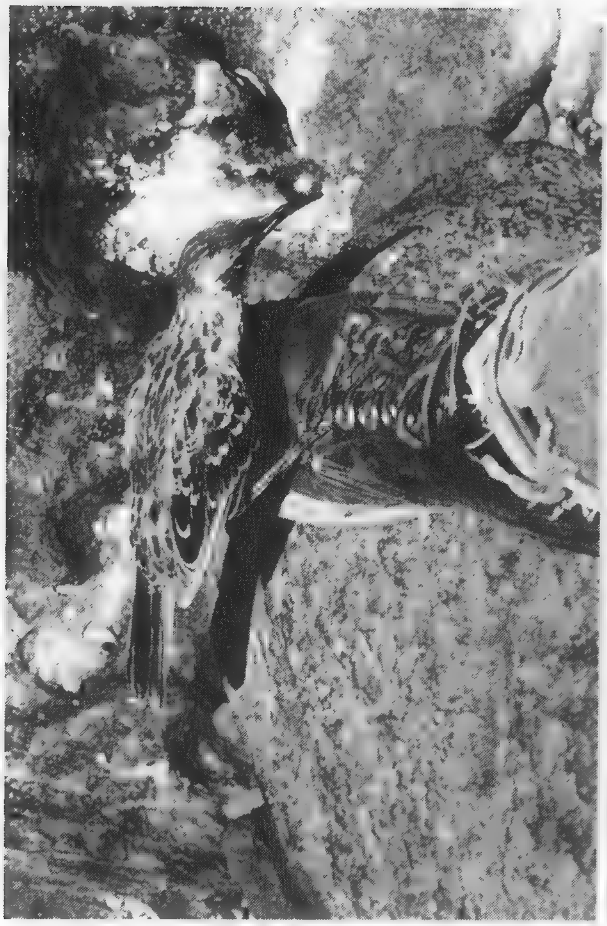
[b] R. I. Bowman, field observations, January 1964.

[c] Lévêque, 1964.

[d] Nelson, 1968.

[e] Beebe, 1924.

[f] X = breeding colony, size unknown.



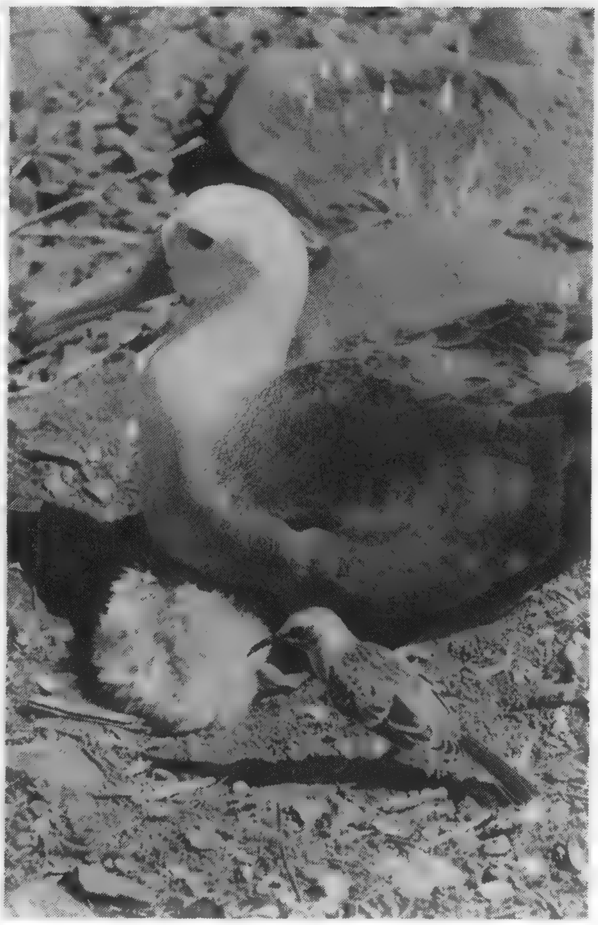


Figure 15 (*left*). An immature mockingbird. *Nesomimus macdonaldi,* on Hood Island examines shiny boot eyelets which it subsequently probed with the bill.

Figure 16 (*right*). An adult *Nesomimus macdonaldi* on Hood Island preparing to peck the cloacal region of downy Waved Albatross while parent looks on without intervening.

eggs and killing the young of the Masked Booby. The Long-tailed Mockingbird (*Mimus longicaudatus platensis*) on Isla Plata, however, showed no interest in the eggs of the nesting Masked Boobies. The population of Long-tailed Mockingbirds on this island has the longest bills of any of the species (Chapman, 1926:577), which ranges from coastal Ecuador south through western Peru (Meyer de Schauensee, 1966:410). Under a variety of experimental conditions in our San Francisco aviaries, the Long-tailed Mockingbird from Guayas Province, Ecuador, likewise showed no interest in eggs (Table 5).

Genetics of Mockingbirds

All our efforts to interbreed various racial forms of *Nesomimus parvulus* with *N. trifasciatus* and *N. macdonaldi* were unsuccessful. Ironically, and quite by accident, we successfully hybridized a female Galapagos mockingbird (*N. parvulus*) from Indefatigable Island with a male Long-tailed Mockingbird (*Mimus longicaudatus punensis*) from the mainland of Ecuador and raised one of the hybrid progeny to adulthood. When tested with Egg-type A, plain white, under both normal and fasting conditions, it showed no response, and in this regard, resembled the behavior of the parental male (*M. longicaudatus*).

This experiment suggests, but by no means proves, that the egg-pecking behavior in Galapagos mimids has a genetic component, apparently absent in the continental species. By contrast, the "wing-flashing" behavior, a distinctive response to a strange situation or a potential predator and known to occur in a number of North American mimids (Hicks, 1955; Michael, 1970; Selander and Hunter, 1960), appears not only in the Long-tailed Mockingbird but also in all species of Galapagos mockingbirds (*Nesomimus* spp.) plus our hybrid (*Nesomimus* × *Mimus*).

The least that might be said about the production of our hybrid mockingbird is that the Galapagos species very likely originated from the Long-tailed Mockingbird of coastal Ecuador, and that *Nesomimus* is probably not a valid genus — a criticism originally set forth by Rothschild and Hartert (1899:142). It also appears, that Meyer de Schauensee (1966:viii) erred when he stated that "... the birds inhabiting the [Galapagos] archipelago have probably little to do with South America."

Future Trends in Egg-pecking Behavior

At present the impact of egg-pecking by Galapagos mockingbirds on the reproductive success of seabirds is insignificant. However, it is conceivable that should there be a major buildup of chlorinated hydrocarbons in the ocean environment about the Galapagos, we might expect a concomitant thinning of eggshells, such as has been documented in other seabirds of the Pacific (Risebrough, Mensel, *et al.*, 1967; Risebrough, Reiche, *et al.*, 1968; and Peakall and Lincer, 1970). The fact that yellowfin tuna (*Thunnus albacares*), captured in the Galapagos region in recent years, show a significant level of DDT in their tissues (Risebrough, 1969) indicates our reason for concern about future trends in egg mortality in Galapagos seabirds. We should view with alarm any unexpected increase in mockingbird attacks, particularly on Hood Island, until it is definitely established that halogenated hydrocarbon pollutants are not involved or that nesting birds are not being subjected to excessive disturbance by humans associated with burgeoning tourism in the islands.

Summary and Conclusions

Experiments with captive individuals show significant differences in the amount of egg-pecking responses between three species of Galapagos mockingbirds (*Nesomimus*). Under normal feeding conditions, the most responsive species tested was *N. macdonaldi,* Hood Island, followed in order of decreasing responsiveness by *N. trifasciatus,* Champion Island, and *N. p. parvulus,* Indefatigable Island. These results parallel field impressions of the three species' readiness to peck seabird eggs.

Hunger, prompted by 24 hours of fasting, increased search activity in all three species tested, but the greatest increase occurred in *N. trifasciatus* and *N. p. parvulus.* The most responsive species, *N. macdonaldi,* showed a lower threshold for food selectivity under a fasting regime. In the most recalcitrant species, *N. p. parvulus* and *N. trifasciatus,* learning appeared to play a significant role in the development of the egg-eating habit.

The low threshold of response to egg-pecking in *N. macdonaldi* appears to be associated with the high frequency of exposure to seabird eggs under natural conditions on Hood Island. The high threshold of response in *N. p. parvulus* may be correlated with the very low frequency of exposure to seabird eggs on Indefatigable Island.

The tendency to peck seabird eggs prevails among those mockingbird populations that have comparatively long bills and that live on the smaller low-lying arid islands, where a multitude of seabirds come to nest amid a flora that is depauperate in species.

The Long-tailed Mockingbird (*Mimus longicaudatus*) from continental Ecuador displays no propensity for egg-pecking, either in its natural environment or in captivity. A hybrid between a Galapagos mockingbird and a Long-tailed Mockingbird (female *Nesomimus parvulus parvulus* × male *Mimus longicaudatus punensis*) also failed to peck eggs, even after 24 hours of fasting.

Acknowledgments

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GROOMING BEHAVIORS OF THE BLUE JAY

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Drawings by W. C. DILGER

The feathers of the bird serve not one but a number of quite different functions. As insulators they protect the body from extremes in temperatures; as extensions of the wings and tail they provide flight surfaces. At the same time their colors and color patterns aid in the performance of many behaviors — social, agonistic, reproductive, and cryptic, to name a few. The bird must therefore maintain its feathers in the best possible condition at all times. It must also take care of its skin, scales, and other integumental structures. To this end birds have evolved certain grooming behaviors, sometimes termed toilet behaviors, which Andrew (1956) defined as "behavior directed to the care of the body surface." I consider preening, feather-settling, scratching, bathing, and bill-wiping to be toilet behaviors and add to this list anting and sunning, although I am not sure of their roles in maintaining feathers and integument. This paper constitutes a description of the toilet behaviors in the Blue Jay (*Cyanocitta cristata*).

Methods of Study

I observed Blue Jays, both captive and wild, from September 1962 through 1964 and kept a male bird (RB 2) at home during the first year of the study. An outdoor flight cage held 12 captive birds, nine of which I obtained as nestlings and hand-reared until they were self-sufficient in the cage. This enclosure, 32 by 28 by 8 feet in size, and covered with a 1 by 1.5-inch welded galvanized wire, contained a small pool, numerous logs, stumps, bushes, and several small trees, and, except for a roof partially covering one end, was open to the sky in all weather. Since it connected to the "Owl House" at the Cornell University Laboratory of Ornithology, I watched the birds from a small office in that building. I also observed 35 wild jays in the neighboring woodlots near the Cornell campus in Ithaca, New York. In keeping my records, I used a field notebook, a tape recorder, a 35 mm still camera, and a 16 mm motion-picture camera.

The regular diet of the captive birds consisted of a canned dog food, cuttlebone, boiled chicken eggs, raw beef liver, an insectivorous bird mixture developed by Ficken and Dilger (1961), French's parrot seed mixture, cracked corn, grit, acorns in season, and peanuts, suet, and vitamins during the winter. In addition, the birds fed on various insects that entered the flight cage and the fruits, flowers, and leaves of plants in the enclosure. All the captive birds rapidly gained weight when young and maintained normal adult weights during the course of the study.

Preening

Preening occurs most frequently after bathing and before resting or roosting for the night. In juvenile jays, preening differs from that in adults in two ways: First, the young are uncoordinated, whereas the adults are adept.

Preening begins in nestlings shortly before the feathers break through the sheaths and seems to assist in removing the sheaths (Ficken, 1962). They preen when they are not sleeping or eating, and their preening improves so much with age and practice that, by the time they leave the nest, they preen almost as efficiently as the adults. Second, the nestlings eat the feather sheaths after the feathers have broken through; the adults do not. The eating of feathers is not uncommon. Whereas I noted it only in juvenile Blue Jays, William C. Dilger (pers. commun.) has seen both juvenile and adult thrushes (*Catharus* spp. and *Hylocichla* sp.) eat feathers and feather sheaths. This habit may conserve proteins important for feather production in birds that molt rapidly or in young that must acquire feathers quickly. The eating of feathers may also be important in the synthesis of Vitamin D (Kelso, 1946).

The motions employed by a Blue Jay in preening various parts of the body differ according to the location of the feathers it is working on. In preening a typical body contour feather, the bird opens its bill, takes hold of the shaft at the base (the calamus), and strokes the feather with a slight nibbling or twisting motion from base to apex, thereby running the barbs through the bill and smoothing, straightening, and bringing them together so that they interlock.

During preening, three basic positions of the head enable the bird to reach various parts of the skin or integument: (1) the head turned over the left or right shoulder; (2) the head turned sideways toward the wings; (3) the head oriented downward and backward. The bird slightly elevates the body feathers while preening and, between preening sequences, may settle the feathers in different parts of the body.

When the bird turns the head over the shoulder and reaches toward the tail, it spreads the flight feathers (rectrices) and turns them to one side. It then grasps a rectrix and strokes it. As the bill moves from the base to the apex of the rectrix, the bird brings the tail back into line with the body axis and, at the same time, brings the head back somewhat laterally to its normal position. The feather, pulled from place during this action, returns to its normal position.

The bird also reaches the rump and area of the vent by extending the head over one shoulder. While the head is turning, it raises and turns the tail to the same side. With the tail in this position, the bird can preen the rump or extract oil from the uropygial gland. When preening the under tail coverts or the crissum, the tail turns to the side as the head comes over the shoulder and back, and the vent region turns so that the crissum becomes a lateral surface. The wing is lowered out of the way, enabling the bird to preen the vent region readily. The bird also preens the rest of the back and the scapulars by reaching over its right or left shoulder and nibbling each feather.

The Blue Jay turns its head back to preen the breast, belly, and side. It arches its neck sharply near the head to preen the anterior breast or axillary feathers, but when preening farther back on the belly or flanks, it arches its neck nearer to the shoulder. To preen the axillary, side, or flank feathers, the bird moves the wing to the side and away from the body so that it can grasp the feathers without hindrance from the wing.

To preen the wings and sides of the neck, the bird turns its head and reaches to the side. It reaches various parts of the wing by coordinated movements of the head and wing, turning the head and orienting toward the wing. If the bird is preening the wing coverts or wrist, it draws slightly away from the wing and inserts the bill into the feathers as the wing moves forward. The jay preens these feathers beginning with the leading edge of the wing and working toward the last row of coverts next to the trailing edge. It raises the pollex, or "thumb," and extends the wrist just far enough to grasp the alular quills. The bird preens the flight feathers (remiges) by holding the wing toward the front and away from the body so that it can reach the most distal primary on the under surface. It strokes the remiges from the calamus to the tip in the same way as the body contour feathers. As it raises the wing, the feather passes through the downstroking bill. I never saw Blue Jays preening the remiges from the upper surface.

To preen the tarsi or toes, the jay tips slightly forward, flexing the neck and lowering the head to touch the toes. It then grasps the scale or scales and nibbles, pulling and twisting them. Sometimes the bird preens only a scale or two in this manner, and sometimes it runs its bill along the full length of the tarsus or toes, covering all of the scales in one sequence. Often it extends the toes briefly during this activity.

In discussing the sequence of preening the various body regions, Coutlee (1963) suggested that the sequences are random among goldfinches, but that once a bird has preened a particular area there is a tendency to preen the adjacent area. My observations of preening sequences in Blue Jays indicate the same tendency.

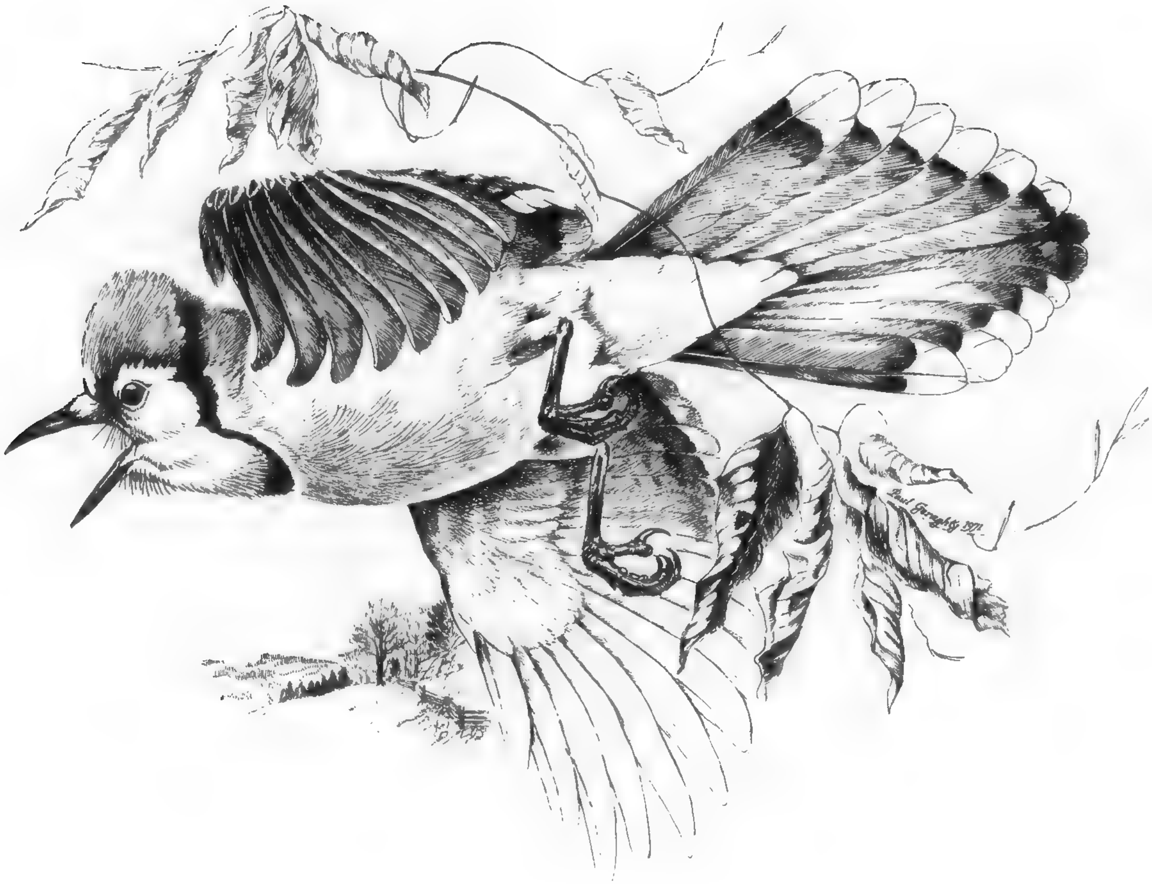
Scratching

Scratching alleviates irritation about the head and neck (Nice and Schantz, 1959) and permits the jay to maintain those parts of the head and neck that it cannot reach with the bill. Blue Jays scratch by lowering the wing with the tip slightly extended and shifting the weight from the scratching foot to the opposite foot. The scratching foot reaches over the lowered wing as the bird tilts its head to the side and moves its back to meet the foot. The leg repeatedly reaches and flexes very rapidly. Thus, adult Blue Jays scratch indirectly with the foot over the wing; juveniles at times scratch directly, with the foot under the wing. The jay turns, twists, or rotates its head to scratch the bill, nasal bristles, crown, nape, chin, eyes, and auriculars with the toenails. When preening around the eyes, the bird rotates the head so that the toenails strike all of the circling feathers. Curiously enough, instead of the toenails moving around the eye, the eye moves around the toenails. Usually, the jay raises the crest partly or fully when scratching the head.

In addition to scratching, the jay also removes irritants or grooms the head, particularly around the base of the bill and back to the auriculars, by rubbing these areas on a perch or edge. This movement is similar to bill-wiping, except that it is slower.

Feather-settling

Blue Jays fluff and shake their body contour and flight feathers both during and after preening and bathing. They fluff the body feathers first and then shake from side to side. The shaking begins at the head and moves back, increasing in amplitude and decreasing in frequency, so that the tips of the rectrices, moving from one side to the other and back again, describe a wide arc. As the body swings to one side during this shaking, the wing on that side may drop several millimeters. As the body swings back to the other side, the



Blue Jay, *Cyanocitta cristata*.
Drawing by Paul Geraghty.

wing returns to its normal position and the wing on the other side drops momentarily. The size of the arc described by the tip of the rectrices seems to indicate the intensity of feather-settling. Presumably, feather-settling readjusts the feathers following a disruption of their normal position.

Bill-wiping and Bill-cleaning

Bill-wiping always occurs after a Blue Jay has finished eating a morsel. The bird generally wipes the bill on an edge or on its perch by orienting its body toward the side, tipping forward, and extending the neck and head so that the bill touches the edge. Then it rubs the bill up and down the edge, first on one side and then on the other. The action is like a butcher sharpening a knife on a butcher's steel. Sometimes the bird dislodges foreign particles clinging to the bill, or discards food items from the mouth, by flicking the head to the side as it bill-wipes.

Nestling and fledgling jays often clean their bills by running their tongues along the cutting edge (tomium) from back to front on one side and then from front to back on the other. This action is rare in adult jays. Rand (1937) also reported this cleaning activity, noting that this use of the tongue was not common in young captive birds after 33 days.

Bathing

After a young bird's first bathing experience, it bathes regularly from one to three times a day. Rand (1937) saw his young jays bathing for the first time when they were 28 days old. I observed the first bathing in my captive jays when they were between 21 and 30 days old. The first few times they bathed, they became so wet they could not fly. Thereafter, they usually stopped before becoming too wet. Only occasionally during the next year did a young jay so drench its feathers that flight was almost impossible. In the second summer, I never saw a jay bathe until it was too wet to fly. The captive jays bathed readily at any time of the year and in almost anything — snow or rain, pools or puddles. However, in the winter they never entered the water, as they frequently did during the summer. Instead, they perched at the edge of the pond, carefully keeping feet, tail, and ventral feathers out of the water.

I observed two bathing patterns: "splash-bathing" and bathing. The jay always drinks before bathing or splash-bathing and usually makes dry-run bathing movements before bathing, but rarely before splash-bathing. The bird begins splash-bathing perched at the edge of the water. It drinks, flexes its legs, leans forward, dips its bill into the water up to the base of the nasal bristles, and then begins to shake its head vigorously from side to side in a 180 to 220-degree arc, splashing water on the throat and over the back and wings. As the water strikes the bird, it fluffs the anterior feathers, moves the wings out and away from the back, and holds the wrists from two to three centimeters away from the body. It flutters its wing-tips up and down, adding to the water splashed by the head. During these actions, the tail is closed and the crest flat or only partly raised. The splashing dampens the feathers of the face, throat, and wing-tips. After the initial dip, the bird extends the legs to their normal perching position, folds the wings, flattens its crest if it was raised, and settles the feathers. The jay may then fly to a perch nearby, settle its feathers again, and preen, or it may return to the water and take several more dips.

Bathing begins in the manner described for splash-bathing, but in this case the bird hops into shallow water, fluffing the ventral feathers and keeping the tail and head well above the surface. The bill and face are immersed up to or above the eyes. As the bird splashes water in the manner described above, it flutters the wings in the water and lowers and spreads the tail so that it is on or beneath the water surface, thereby immersing the crissum and ventral feathers. It vigorously shakes its head, wings, and tail in a manner suggesting an exaggerated feather-settling. When the bird stops shaking, it frequently spreads its tail on the surface of the water with the wing-tips in or on the water. When the jay raises its head, the crest and contour feathers remain fluffed. The bird may stand in the water, shaking and fluttering in this position for three or four different splashing and shaking sequences. Then, returning the wings to their normal position, the jay flies laboriously to a perch nearby, where it preens and oils its feathers.

Bathing sometimes follows splash-bathing, and the two may intergrade. For example, the movements described as head movements in bathing sometimes accompany wing or tail movements in splash-bathing. Generally these two bathing patterns, which may represent bathing intensities, are distinct.

Bathing intention movements — feather fluffing and wing and tail flutterings — are seen before a bird enters the water or even between dips in the water. The crest is usually raised during this activity. One may elicit these intention movements and subsequent bathing activities in jays merely by dripping or splashing water, or the bathing of other birds may stimulate them.

The movements in rain-bathing are similar to bathing intention movements. In the rain, however, the bird perches on a branch and shakes its head from side to side as though it were in the water, though the arc described by the head does not appear to be as large as in bathing intention movements. Occasionally, when bathing in the rain, jays omit the head movements characteristic of bathing and only flutter the wings and tail.

I saw snow-bathing only in the captive birds. The movements are similar to those of splash-bathing, except that the bird stands in snow. The jay sticks its head into the snow and shakes it, flutters the wings, and fluffs the breast feathers. A snow bath does not last as long as a water bath. I saw marks of snow-bathing more often than I saw birds taking snow baths, and the marks indicated that snow baths are frequent and depend on snow conditions. For example, I always saw snow baths or fresh marks from snow-bathing after a recent fall of powder snow.

Sunning

In sunning, the jay uses feather and limb postures suggestive of toilet behaviors, indicating to me that sunning may be important in the maintenance of the feathers or the integument. The feather ruffling and gaping during sunning may also be partly a response for regulating body temperature (Rand, 1937; Hauser, 1957). Lanyon (1958) suggested that heat alone may elicit the sunning position. This possibility, if true, does not necessarily mean that heat regulation is the sole function of sunning (if a function at all).

Kelso's observation (1946), that the Vitamin D precursor — ergosterol — found in the oil of the uropygial gland is applied to the feathers during preening, suggests another possible function of sunning. He thought that the birds may swallow Vitamin D or its precursor when anting. It seems likely to me that sunning, rather than anting, leads to the synthesis of Vitamin D by ingestion of the oil applied to the feathers or by the eating of the feathers themselves. After this ingestion, the exposure of the skin to sunlight may lead to the synthesis of Vitamin D. I shall not undertake here a more complete discussion of the possible functions of sunning. For a review of the literature and a discussion of a number of intriguing questions in connection with sunning activities, see Goodwin (1967), Hauser (1957), and Teager (1967).

Sunning by Blue Jays is, as Rand (1937) also noted, frequently preceded by bathing. I observed two forms of sunning: sunning when on a perch and sunning when on the ground. When sunning on a perch, the bird raises the crest, droops the wings, partly spreads the tail, ruffles the body feathers, and gapes. It tips the head to the side and opens its eyes. The jay always keeps its backbone at an angle to the sun, so that one eye looks in the direction of the sun. The bird may hold this position from a few seconds up to 3.5 minutes. Usually a perched bird suns only on one side.

Sunning on the ground is essentially the same, except that it is more exaggerated. The bird leans to one side, keeping both feet on the ground and spreading its tail widely, ruffles the body feathers, and fully raises the crest. It spreads the wing fully, on the side exposed to the sun, and holds it either on or off the ground, exposing the axillary region, and tilts the head back and to the side away from the sun. It keeps both eyes open, one staring in the direction of the sun, and gapes. It does not seem to face the sun. The jay holds this sunning position from several seconds to four minutes before changing its position and sunning the other side. One bout of sunning on the ground may involve several position changes and last as long as 45 minutes. A thermometer placed on the ground at six sunning sites in the forest immediately following a sunning bout by a jay recorded temperatures ranging from 34°–44°C (93.2°–111.2°F) in direct sunlight.

Hauser (1957) discussed four different levels of response to the sun and reported that she observed Blue Jays at all four of these levels. I suspect that Hauser's first level is entirely a thermoregulatory response, made by a bird under heat stress, while her other three levels are at least in part sunning positions, held by the bird under stimuli not directly related to thermoregulation. Levels II and III probably correspond to the two positions I have described as "sunning," except that the body feathers of the Blue Jay are ruffled rather than fluffed, as she states. I did not observe, in either captive or wild jays, her highest intensity, Level IV, during which the bird is completely spread out with both wings and the tail fully extended on the ground.

Anting

According to Simmons (1959): "Anting consists of certain stereotyped movements used by passerine birds in relation to ants (Hymenoptera: Formicidae), chiefly the non-stinging, acid-spraying members of the subfamily Formicinae. This unique behavior results in the bird's plumage being anointed with organic liquids, mainly formic acid, although it is disputed whether this effect is primary or merely incidental." Since Chisholm's discussion (1934; cited by Simmons, 1957), anting has been the subject of much speculation. Simmons (1966) estimated that over 210 species of passerine birds ant; many authors, mostly amateurs and aviculturalists, have described anting in various species of birds. Two principal kinds of anting behavior are recognized: ant-application or active anting, in which a bird actually applies ants directly to its

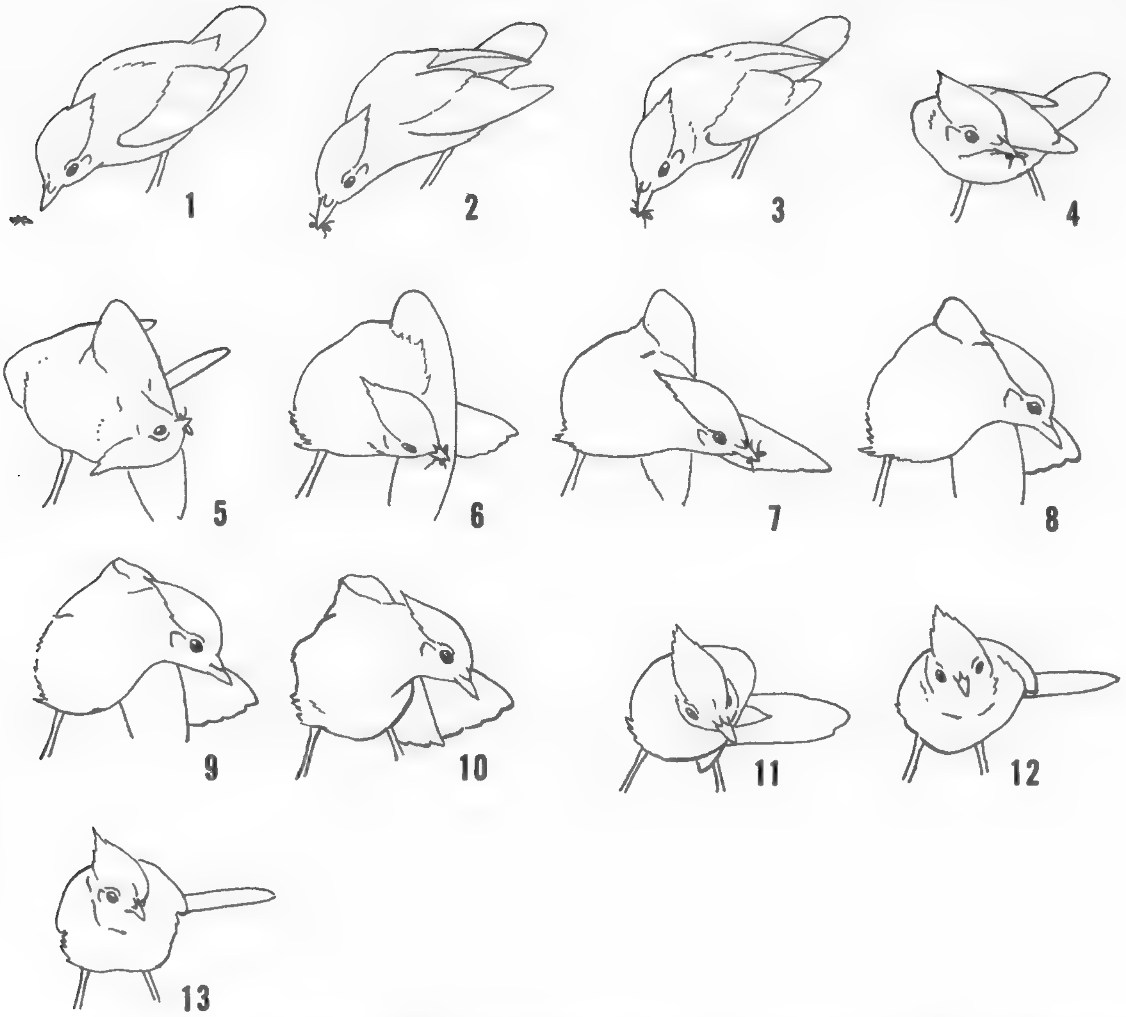


Figure 1. Anting sequence drawn from a high-speed motion-picture film. During the application of the ant to the wing, the bird wipes the ant along the remiges in a manner suggesting bill-wiping. No contact is made with the crissum or rectrices. Note that the jay discards the ant in frame 8. Nine frames separate each drawing. Drawings by W. C. Dilger.

plumage; and ant-exposure or passive anting, in which a bird merely allows ants to roam through its ruffled plumage.

Many authors have described objects used by birds for anting. Brackbill (1948), Groskin (1950), and Whitaker (1957) published lists of ant species used. Birds sometimes perform anting behavior using substitutes for ants. The list of over 40 ant substitutes includes tobacco smoke (Ivor, 1958; Miller, 1952), burning straw (Burton, 1957), sawdust (Hailman, 1960), dermapterans (Poulsen, 1956), snails (Terres, 1962), hot chocolate and soap suds (Nice, 1955). An extensive list of these substitutes may be found in Poulsen (1956) and Whitaker (1957). What it is about these varied substitutes that elicits anting in birds is unknown. Whitaker (1957) suggested that such substitutes may have "thermogenetic" (heat producing) properties.

Perhaps the most controversial aspect of anting is its function and biological significance. The many explanations include food transport (F. C. Delorme, cited in Chisholm, 1944), food cleansing (Poulsen, 1955), and autoeroticism (Whitaker, 1957). The most popular explanation is that birds use ants to control or remove ectoparasites (Goodwin, 1955; Groskin, 1950). It is apparent that some of these hypotheses are more subject to empirical testing and analysis than others. Whitaker (1957) and Holgersen (1958) present a more complete list of hypotheses and a discussion of each. A few persons who have experimented on anting have reached different conclusions regarding its significance. Chisholm (1959), Holgersen (1958), Simmons (1957; 1966), and Whitaker (1957) provide summaries and bibliographies on anting.

That Blue Jays actively ant was rather vividly brought to my attention in several instances involving bird RB 2, the captive hand-reared male kept at my home. RB 2 first anted when he was approximately 63 days old, using tobacco taken from a long-stemmed pipe in my mouth. Unfortunately, the smoke, burning tobacco, hot ashes, and the intense activity of the bird perched two inches from my face obscured a clear view of the proceedings. Later, he anted using burned tobacco and pipe ashes. However, it was not until the following spring (1963) that he gave a prolonged performance.

> 13 March 1963, 18:15: RB 2 landed on the edge of a dish of sweet cucumber pickles. He looked into the dish with first one eye and then the other. He then took a pickle slice and began applying it to his left wing and tail. This activity was clumsy and the bird toppled from the edge of the dish. Subsequently, he returned to the edge of the pickle dish, began picking out the cucumber seeds floating in the juice, and applied them to the wings and tail. He continued this activity, uninterrupted, for 32 minutes. At the end of this time the bird was completely drenched with pickle juice. Extensive preening and bathing followed.

Another captive jay anted with ants of an unknown species when 69 days old. Similarly, Hardy (1961) reported that his captive Blue Jay first anted when about 57 days old.

During August, September, and October 1963, I made 20 attempts to induce the 12 captive Blue Jays in the flight at the Laboratory to ant and recorded 10 successful trials with a high-speed 16 mm motion-picture camera. The five species of ants that elicited anting in the captive Blue Jays were: *Acanthomyops claviger, Camponotus noveboracensis, Creamotogaster lineolata, Formica integra,* and *F. pallidifulva.* Ants of the *Formica* "fusca group" did not stimulate anting in my birds, although Whitaker (1957) listed them as one of the species groups that has elicited anting.

A Blue Jay begins to ant standing on the ground (Figure 1). It approaches the ants with its body feathers sleeked, crest flattened, and neck erect with the head turned down toward the ants on the ground. The bird moves the wings outward slightly, drooping them toward the ground and away from its body so that the tips of the primaries sometimes actually touch the ground between the feet and the tail. It holds the tail directly in line with the long body axis and often presses the tip to the ground. The bird stretches out its head and picks up, bites, and drops ants in rapid succession before retaining any of them in its bill. During active anting sequences, I saw Blue Jays sometimes holding one and sometimes several ants in the bill.

The active sequence of anointing the remiges involves the bird's picking up the ant or ants, wiping them on the remiges, returning the head forward, and either discarding or eating them. The jay holds the ants by the head or thorax with the abdomen hanging free from the tip of the bill. As the bird begins to turn the head toward the wing to be anted, it moves the tail and wing simultaneously, twisting the tail toward the side to be anted and presenting the under tail coverts as a lateral surface. It moves the wing farther outward, raising the wrist toward the bill while bracing the tips of the primaries against the base of the rectrices and under tail coverts. The long body axis is U-shaped as the bird begins the wiping stroke on the remiges. The bird strokes one or two feathers with the abdomen, or gaster, of the ant in a motion very similar to bill-wiping, beginning at the base of the shaft and continuing to the tip of the remex. During this action the tip of the bill often brushes the feathers. When the bill reaches the end of the stroke, it may continue the wiping motion in the space between the braced wing and feet. In this way the bird sprays the under tail coverts, crissum, and flanks with the ant's defensive secretions.

Frequently during the activity the bird extends the opposite wing briefly for balance, and sometimes moves the opposite foot laterally away from the anted side and moves the foot on the anted side closer to the wing and tail. If either foot steps on a wing or the tail during the recovery from anting, the bird may lose its balance and tumble over. In recovery, the bird brings the head forward and returns the wings to their original position. The bird may leave the tail slightly extended toward the anted side or return it to its former position. I noted that the nictitating membranes covered the eyes as the bird picked up the ants and applied them to the remiges. Unfortunately, I could not accurately determine the coordination of the movements of the membranes with the other actions.

In 136 filmed sequences of anting, the birds discarded the ants 82 per cent of the time after using them and ate them 9 per cent of the time. I could not determine the disposition of the ants in the other 9 per cent of the cases. The jays used an ant only once in 73 per cent of the anting sequences. However, some ants, 17 per cent, were used twice; 9 per cent, three times; and 1 per cent, four times. The average sequence of active anting took about 0.5 second, ranging from 0.33 to 1.0 second. Single bouts of anting sequences ranged from one to 45 minutes for individual birds. Other authors (cited by Holgersen, 1958) have noted a similar range for one bout of anting. Preening and occasionally bathing typically follow a bout of anting.

Many authors indicated that birds actively ant the tail and under tail coverts as well as the wings, and this was my impression before viewing the high-speed motion-picture films. But after a careful examination of these motion-picture films with a time-motion projector, I discovered that the captive Blue Jays did not ant the tail or vent region directly. On examining published still photographs of anting Blue Jays and other birds, particularly in Ivor (1956), Simmons (1957), and Whitaker (1957), I found that they showed only direct anting of the wings. Unfortunately, only single photographs are given, and the direction of the movement of the head and bill cannot be determined. Since I saw no clear evidence that the birds in the pictures were directly anointing the tail region, apart from the remiges, I question the conclusion that the tail is anointed directly. Because of the high speed of anting activity, one must recognize the possibility of error in observations. Only the high-speed motion-picture films, viewed carefully frame by frame in the time-motion projector, led me to change my initial impression that the birds anoint both wings and tail. I might mention that when Blue Jays preen the tail or vent region, they stretch the head over the shoulder and back and lower the wing out of the way. When jays preen the remiges, on the other hand, they do so from the under side, raising the wing laterally away from the body. Thus, the position of the wings and the head in the anting activity is similar to the usual method of preening the remiges. This similarity tends to support the conclusion that Blue Jays, and perhaps other passerines as well, direct anting primarily to the flight feathers of the wings, and that the tail and vent regions receive the ant secretions only indirectly. Simmons (1959; 1966) argued, for other reasons, that anting is directed primarily to the wings. Of course, preening after anting probably distributes the ant secretions to other parts of the plumage in addition to the wings and tail.

On the basis of the preceding observations of anting, I should like to speculate about the function and biological significance of this intriguing behavior. E. M. Boyd, in her review of bird ectoparasites (1951), reported that some amblyceran lice are haematophagous (blood-eating), typically occurring "between the skin and quill," and that certain feather-dwelling, and perhaps feather-eating, mites (Acarina, Analgesidae, and allies) occur on the remiges and under wing coverts, spreading to the body feathers when population densities are high. She further reported that she found blood-sucking mites of the superfamily Parasitoidea on the skin of the wings and vent regions.

Many ectoparasitic lice and mites are host-specific, and most birds probably harbor more than one species, each usually being confined to a particular region of its host's body. Unfortunately, much of the information available on bird ectoparasites concerns domesticated birds, and little is known of the biology and life cycles of the ectoparasites on wild birds. However, "The Merck Veterinary Manual" (1955), based mainly on domesticated birds, states that haematophagous ectoparasites (apparently parasitoid mites) can cause intense skin and feather follicle irritations and frequently result in the bird's plucking at the irritated areas, causing feather loss. Further, high densities of mites can cause anemia and emaciation that may reduce egg production. These ectoparasites may also carry diseases.

Boyd (1951) noted that among passerine birds the heaviest infestations of ectoparasites occur in the Hirundinidae, Corvidae, Laniidae, Sturnidae, Vireonidae, and Icteridae. Whitaker's list of bird species that ant, representing 23 passerine families, shows that roughly 40 per cent of the observations of anting birds were species belonging to the Corvidae, Icteridae, and Sturnidae. Coincidental as this finding may be, I suggest that it reflects an association between anting and ectoparasite infestation. An observation by the Russian acarologist, V. B. Dubinin (*in* Kelso and Nice, 1963), supports this conjecture. Dubinin collected four anting Meadow Pipits (*Anthus pratensis*) and found that approximately 35 per cent of the mites on these birds were dead 12 hours after anting; then he collected four Meadow Pipits that were not anting and found only 0.6 per cent of the mites died in the same period of time.

Persons who race pigeons are well aware that they should not fly the birds when the distal remiges are in molt or the birds heavily infested with ectoparasites. Energy drain from molt, a weakened condition resulting from ectoparasite infestation, or extra holes in the wings caused by feather loss significantly reduce the pigeon's flight speed. Therefore, it is not profitable for the racer to fly his birds in competition. The removal of ectoparasites increases the bird's efficiency in flight, and anting may well serve in this removal. Simmons (1966) also contended that anting may function, at least in part, to augment preening in the control or regulation of ectoparasites.

The skin and follicle irritation, feather loss, anemia, or emaciation resulting from ectoparasite infestations seriously limit the effectiveness of the bird in coping with its environment. One might surmise that it would be to the selective advantage of the passerine species to evolve an adaptation that reduces infestations of ectoparasites, and one must assume that ectoparasites occur on all parts of a bird's body. Why, then, do Blue Jays ant only the wings? I suggest two answers: First, mite infestations of the wing may have a more immediate effect on the bird than infestations in other areas of the body, since the loss of several remiges might seriously impair a jay's flight. Not only does a bird with holes in the wings lose wing surface and flight speed, but it also must deal with turbulence, created by the holes that probably increases the amount of energy expended for normal flight. The loss of a comparable number of body feathers would not impair the bird's effectiveness in coping with the environment as seriously as would the loss of flight feathers. Second, the wing in its normal motion probably touches more body feathers than does any other single part of the bird, and any secretions deposited on the wing will rub off on more feathers than if the bird deposited the secretions on, for instance, the breast. Thus, either by contact with the wings or by the bird's preening, most of the feathers receive some of the ant secretions.

Holgersen (1958) cited several authors who indicate that, in northern Europe and North America, anting seems to occur more frequently during the summer months. Similarly, Potter (1970) indicated that anting activity reaches a peak in August. Boyd (1951) reported that lice and feather-eating mites occur on birds in greater concentrations during the warmer seasons, and also noted that there is a sharp drop in their numbers following the prebasic (post-nuptial) molt of the summer. If anting occurs more frequently in the summer months, it is not only because the birds are more likely to find active ants at that time, but also because the parasite populations are at their seasonal peak. Anting in the summer would tend to reduce the number of parasites transmitted both from parent birds to their offspring and from old feathers to new.

I have argued here for the ectoparasite-regulation function of anting. Obviously, information regarding the biological significance of anting is sketchy and inconclusive. More observational and experimental information is needed before one can accept or reject the hypothesis that anting serves to reduce or regulate ectoparasites.

Epilogue

The toilet behaviors of a bird or any animal constitute only a portion of the day's activities. Since many observers find such maintenance activities routine and repetitious, or even uninteresting, these behaviors are studied less than the more elaborate or unusual behavior patterns. Yet the routine maintenance behaviors are important. Often they are the building blocks for more elaborate activities, as in the case of the preening activities in anting. These maintenance behaviors may also provide insights into questions of environmental adaptations and evolutionary relationships. Careful and detailed descriptions of these activities establish basic facts concerning the biology of an animal. Unfortunately, because detailed descriptions of behavior are so time consuming, professional biologists often neglect them. The beginning student or the serious hobbyist can make a substantial contribution to the study of birds by providing careful descriptions from which the professional biologist can extract hypotheses for specific and theoretical studies.

Summary

Grooming or toilet behaviors are those directed to the care of the body surface — feathers, skin, and other integumental structures. This paper is based on a study of such behaviors in twelve captive and 30 to 35 wild adult

Blue Jays (*Cyanocitta cristata*) and the situations in which the birds employ these behaviors. Reference is made to some juvenile behaviors when they differ notably from adult behaviors.

The jays used three basic head positions in preening different topographic regions of the body. Nestling jays ate feather sheaths in preening bouts during the acquisition of juvenal plumage. The jays preened, or scratched the head, by extending the leg over the lowered wing while the head was turned, twisted, or rotated, so that the region being scratched moved around the toenail. Some juveniles scratched the head directly, moving the foot under the wing.

Blue Jays bathed in standing water, rain, or snow. Both bathing and splash-bathing are described.

Sunning bouts varied in duration from a few seconds to 45 minutes. The temperature at the sunning site ranged from 34°–44°C (ca. 93°–111°F). A brief discussion of the possible functions of sunning is presented.

Captive anting Blue Jays were observed directly and filmed with a high-speed motion-picture camera. Filmed sequences of anting were viewed with a time-motion projector. According to these films, Blue Jays apply formicine ants to their remiges in a behavior comprised of components from the remex-preening and bill-wiping behaviors. The biological significance of anting is discussed and arguments are presented in favor of ectoparasite regulation as a function of anting behavior.

Toilet behaviors are the building blocks in more complex behavorial displays, as in the case of preening activities in anting. These behaviors have substantial evolutionary significance, and, as such, they deserve greater study and more precise descriptions. The careful student or layman can often provide such descriptions.

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COVER PAINTING OF THE SOUTHERN HELMETED CURASSOW

ALBERT EARL GILBERT

I made the cover painting of the Southern Helmeted Curassow (*Crax unicornis*) for the forthcoming book "Curassows and Related Birds" by Jean Delacour and Dean Amadon. While working on the color plates for this book I was fortunate enough to see all the genera and most of the species of the Curassow family in life, either in the wild or in captivity. Over the course of two expeditions, I came to know many of these somber toned, yet beautiful, birds as they lived in the volcanic mountain forests, steaming lowland jungles, or dry savannas. Throughout tropical America, they inhabit the fascinating worlds of bromeliads, orchids, lianas, and neblina — wild and remote places only now threatened by the intrusion of man.

The Southern Helmeted Curassow from the mountains of Bolivia eluded me. It is extremely rare, known only from scattered field observations and a very few museum specimens. However, my acquaintance with its close relative, the Northern Helmeted Curassow (*Crax pauxi*) in Venezuela, together with study specimens enabled me to paint a fairly accurate picture of this secretive bird. I have based many of the following remarks on the conclusions of Delacour and Amadon.

The turkey-sized curassows and the smaller guans and chachalacas comprise the family Cracidae, gallinaceous birds found mainly in the forested regions of neotropical America. The 13 curassows fall into four groups: (1) the perhaps primitive little Nocturnal or Russet Curassow (*Nothocrax urumutum*); (2) the Razor-billed Curassow (*Mitu mitu*) and two allied species in which the red bill is laterally compressed or otherwise modified; (3) the two Helmeted Curassows which have a large, hard casque; and (4) the seven "typical" curassows which often have soft, fleshy knobs or wattles and a recurved crest of stiffened feathers.

Some authorities regard the Northern Helmeted Curassow from Venezeula and Colombia and the Southern Helmeted Curassow from Bolivia as subspecies of the same species even though their ranges are separated by a gap of some 1,200 miles. Delacour and Amadon tentatively regard the two as distinct species having an interrupted, and in part relict, distribution down the Andes: ". . . though it is difficult to believe they would not interbreed freely, were their ranges to meet."

The two curassows are very similar in every respect except for the shape of the casque and the feathering of the head. Aside from the great gap in range, the principal character favoring specific separation is the feathering of the head. In the Northern Helmeted Curassow, the feathering is dense and plush with a matt appearance; in the Southern Helmeted Curassow, the crown feathers curl forward with a glossy appearance. The shape of the casque varies geographically in all forms, but the variation is not clinal. A rare rufous phase that occurs in the female *Crax pauxi* is as yet unknown in *Crax unicornis.*

In 1969, John S. Weske and John W. Terborgh (Auk, 88:233–238, 1971) discovered a new form of helmeted curassow in a locality in Peru, about 850 miles north of the type locality of *unicornis* in Bolivia and even more distant from the range of *pauxi* to the north. This was significant. Would the new form bridge the differences between the northern and southern forms and show them to be, indeed, subspecies? Evidently not. Weske and Terborgh concluded that the new form was a race of the Southern Helmeted Curassow and named it *Crax unicornis koepckeae.*

Both species inhabit the dense epiphytic vegetation in humid cloud forests where they are most difficult to observe. Charles Cordier found the Southern Helmeted Curassow in Bolivia between 1,500 and 3,600 feet, inhabiting forests of heavy rainfall in a rugged terrain cut by steep valleys (Animal Kingdom, 74 (2): 9–11, 1971). Though the bird no doubt eats tender leaves and buds, its favorite food is the nuts of the almond tree after they have fallen to the ground.

Probably, like other curassows, the Southern Helmeted Curassow travels in pairs or in small family groups and roosts in trees at night. It weighs about eight pounds; its nest, eggs, and downy young are unknown except perhaps by the Indians who, according to Cordier, fashion, among other things, cigarette lighters from its casque.

The distribution of the helmeted curassows along the Andean chain was almost certainly more continuous in the past. The reasons for this diminution are unknown. Hunting by natives, who in some regions valued the helmets as well as the flesh, is a possibility.

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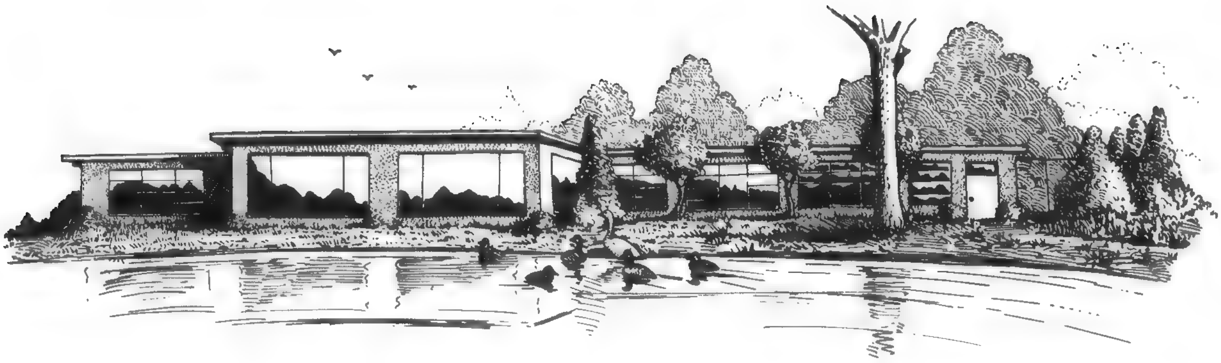

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Boreal Chickadee, *Parus hudsonicus*. Painting by Barry Kent MacKay.

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